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THE OCCURRENCE AND DISTRIBUTION OF THE MAJOR EPIFAUNAL ASSOCIATES OF *FUCUS SERRATUS* L. IN ARGYLL, WESTERN SCOTLAND

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INTRODUCTION

In localities where the influence of wave action is moderated, rocky coastlines in north temperate latitudes are generally dominated by large brown seaweeds. These macroalgae exhibit a distinctive pattern of zonation within the physical exposure gradient which exists between high and low water marks, and extend into the shallow sublittoral zone (Lewis 1964; Stephenson and Stephenson 1972). The broad, flat, rigid or semi-rigid fronds of these algae provide an array of resources for exploitation by a wide variety of marine invertebrates. Detailed reviews of these epifaunal communities are provided by Hayward (1980) and Seed and O'Connor (1981a).

Amongst the lower shore algae the Serrated Wrack *Fucus serratus* L. is particularly attractive to epifaunal species, and consequently supports a rich and vibrant community which consists principally of sessile filter feeding groups such as bryozoans, serpulids, hydroids, and more occasionally sponges and tunicates. Since this community thus includes species which are likely to enter into direct competition with each other, especially for space - the primary limiting resource in these communities, mechanisms ought to exist whereby component species maintain at least some degree of ecological isolation.

In this paper we document the findings of a survey of the epifaunal associates of *F. serratus* at several contrasted sites in Argyll, western Scotland. The principal objective behind this investigation was to compare the epifaunal community of the Serrated Wrack in this geographical location with similar communities which have previously been described elsewhere (Boaden *et al.* 1975; Seed and O'Connor 1981b; Stebbing 1973; Wood and Seed 1980), and to examine to what extent space can effectively be partitioned amongst the dominant components within this community.

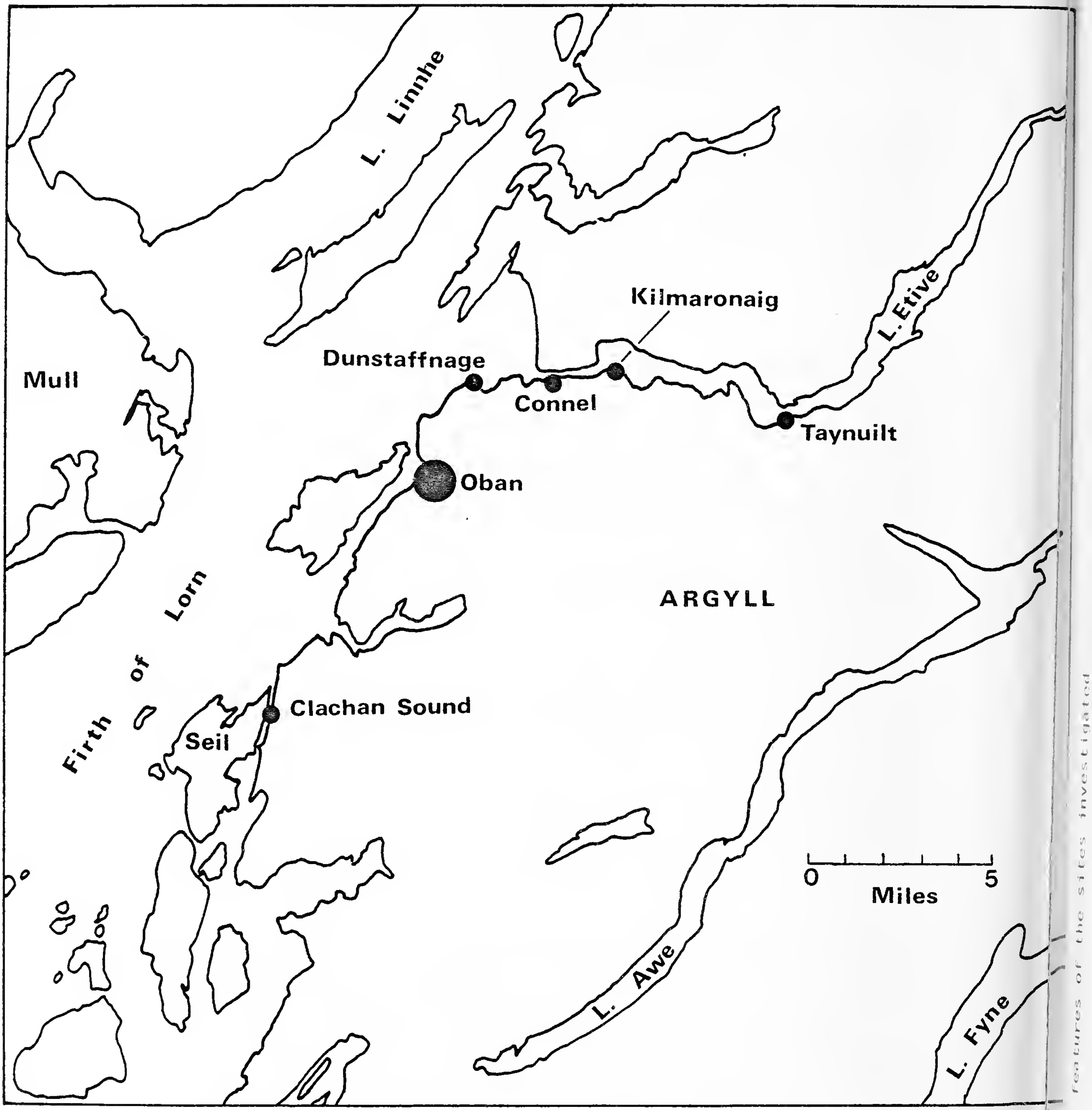

Figure 1
Map showing the location of the sampling sites on the Argyll coast.

Table 1. Characteristic features of the sites investigated

Place Name	Relative abundance of *F. serratus*	General features of the sites
Taynuilt:	Scarce	Flat cobble shore. Small plants attached to jetty. Local abundance of *Fucus ceranoides* and *Enteromorpha* suggest brackish conditions.
Kilmaronaig:	Superabundant	Tidal gully between shoreline and small island. Plants attached to stones and boulders. Some very large *F. serratus* (> 250cm). Moderate current flow over plants on flood tide. Large accumulations of decaying weed.
Connel:	Abundant	Two study sites - Site 1 on landward side and Site 2 on seaward side of a small rocky promontory just below Falls of Laura. Water very turbulent. Plants attached to large stones and exposed bedrock.
Dunstaffnage:		
(a) semi-exposed	Common	Rather steep rocky headland exposed to prevailing onshore winds. Small, abraded plants attached to bedrock. Mid-low shore dominated by *Fucus* sporelings.
(b) sheltered	Abundant	Close to previous site but sheltered from prevailing wind. Rather muddy. Plants attached to boulders, stones or base of rock face.
Clachan Sound:	Superabundant	Narrow tidal gully. Two study sites - Site 1 just below roadbridge, Site 2 slightly to north in the main tidal channel. Plants attached to bedrock and stones amid background of coarse gravel.

STUDY AREAS AND GENERAL METHODS

In June 1977, sixty *F. serratus* plants were collected from eight physically and biologically contrasted sites on the west coast of Argyll. Figure 1 indicates the location of the study areas, and Table 1 briefly documents the main features of each site. At each site, five or ten plants were collected from approximately mean low water of spring tides immediately above the laminarians. Sampling points were chosen arbitrarily within the *F. serratus* zone, although only the most heavily encrusted plants were included in the samples.

Plants were placed individually in separate plastic bags and returned to the laboratory for further investigation. Each plant was immersed in seawater for five minutes, suspended to drain for a further five minutes, and then weighed to the nearest 10g on a Pesola spring balance. Plants were then laid out on a bench and their overall length (cm) recorded. *F. serratus* plants are usually too voluminous to allow study of their total fauna. The longest frond was therefore selected in order to provide information on the distribution of the major species along each plant. This frond was cut up into sections, each consisting of a single Y-shaped dichotomy or segment. Starting from the base of the plant and working towards the distal tip of the frond, these segments were numbered sequentially from Y1 to Yn. The area (A) of each segment face was approximated by the equation

$$A = 2B.L$$

where B is the maximum frond breadth and L the maximum length along either side of the segment. Details of these methods are more fully documented in Boaden *et al.* (1975). Each dichotomy was examined under a stereobinocular microscope, and the associated fauna and flora identified. Since the fronds of *F. serratus* are usually recognisable as being either concave or convex, the fauna and flora of the two faces of each segment were recorded separately. Where this was not possible (especially on the most basal and distal segments) the segment faces were designated concave or convex at random.

Only the most commonly encountered species were quantified. Individual tubes of adult and juvenile *Spirorbis borealis* and the recently settled stages (= ancestrulae) of the bryozoan *Flustrellidra hispida* were counted. For the hydroids, *Dynamena pumila* and *Campanularia flexuosa*, the percentage cover by the colony together with the maximum height of the longest upright branch was noted, whilst for the encrusting bryozoans, *Alcyonidium* spp., *Flustrellidra hispida*, *Electra pilosa* and *Celleporella hyalina*, percentage cover alone was noted.

Epiphytic algae and all other faunal species were simply recorded as present or absent.

Once the longest frond had been carefully removed, the rest of the intact plant was used to test the idea that structural diversity promotes species diversity amongst the epifauna. Structural diversity of each plant (H) was measured by the Shannon-Wiener index (MacArthur 1955)

$$H = -\Sigma p_i \ln p_i$$

where p_i is the proportion of the system in the ith compartment. This was applied to *F. serratus* as follows: each plant in its extended position was cut across its entire width at 15cm intervals and the total foliage of each level weighed. The weight of frond tissue at each level as a proportion of total plant weight then constitutes a p_i in the above equation. Diversity is maximal (H max) when frond tissue is equally distributed between all plant levels. Since this value varies according to the number of levels present, we corrected for the effect of varying plant length by using the value H/H max as a measure of structural diversity. Faunal diversity was simply measured as the mean number of species present per segment face along the longest frond.

RESULTS

Plant size and structure

Our results are based on the analysis of 120 replicates at each Y-level out to and including Y7. Due to the variation in plant size, however, relatively few replicates were available for the more distal plant segments (Table 2). Accordingly, analyses of these more distal dichotomies must be treated with some degree of caution. Three size measurements were recorded for each individual plant: length of the longest frond, total weight, and branching index. These data are summarised in Table 3. The branching index provides some measure of the degree of bushiness within the plants, higher values indicating a greater degree of branching; the weight/length ratio used here is thus analogous to the volume/length ratios which we have used previously (Boaden *et al.* 1975). An analysis of variance showed that intersite differences in plant length, weight and branching index were statistically significant ($F = 5.39$, 7.82 and 10.35 respectively, all at $P < 0.01$). Structural diversity (H/H max) and the number of dichotomies present along the longest frond (Table 3) also showed significant intersite differences when tested by ANOVA ($F = 3.04$ and 2.52, both at $P < 0.05$).

Table 2.

Total numbers (N) of segment faces at each Y level (see text for details) on *Fucus serratus* plants examined during this investigation

Y level	N	Y level	N	Y level	N
1	120	7	120	13	12
2	120	8	102	14	6
3	120	9	80	15	2
4	120	10	68	16	2
5	120	11	44		
6	120	12	24		

Table 3. Sample sizes and characteristics of *F. serratus* at the sites investigated

			Plant (4)					
Site	Plants (1)	Faces (2)	Dichotomies (3)	Length (cm)	Weight (g)	Branching index (g/cm)	Structural diversity (5) H	H/H max
Taynuilt	10	204	10.2(0.4)	79.5(3.3)	363(65)	4.4(0.7)	0.56(0.02)	0.84(0.02)
Kilmaronaig	10	196	9.7(0.6)	109.5(5.6)	1097(154)	9.7(1.0)	0.74(0.03)	0.92(0.01)
Connel								
Site 1	5	80	8.0(0.5)	89.2(3.3)	995(229)	10.9(2.1)	0.61(0.03)	0.85(0.03)
Site 2	5	94	9.4(1.1)	91.4(4.3)	1580(363)	16.7(3.1)	0.67(0.02)	0.92(0.00)
Dunstaffnage								
Sheltered	10	216	10.8(0.5)	93.5(6.6)	583(89)	6.2(0.8)	0.67(0.03)	0.89(0.01)
Semi-exposed	10	172	8.6(0.5)	72.4(2.5)	215(41)	3.0(0.6)	0.56(0.03)	0.85(0.02)
Clachan								
Site 1	5	104	10.4(0.9)	113.3(13.2)	1555(478)	13.1(3.2)	0.73(0.04)	0.90(0.03)
Site 2	5	118	11.8(1.6)	109.7(14.5)	2440(758)	20.0(4.8)	0.64(0.06)	0.90(0.01)

(1) Total number of plants examined.
(2) Total number of segment faces examined.
(3) Number of dichotomies along longest frond. Values are means (±SE).
(4) All values are means (±SE).
(5) Shannon-Wiener Index (H) measured as $-\Sigma p_i \ln p_i$ (see text for details).

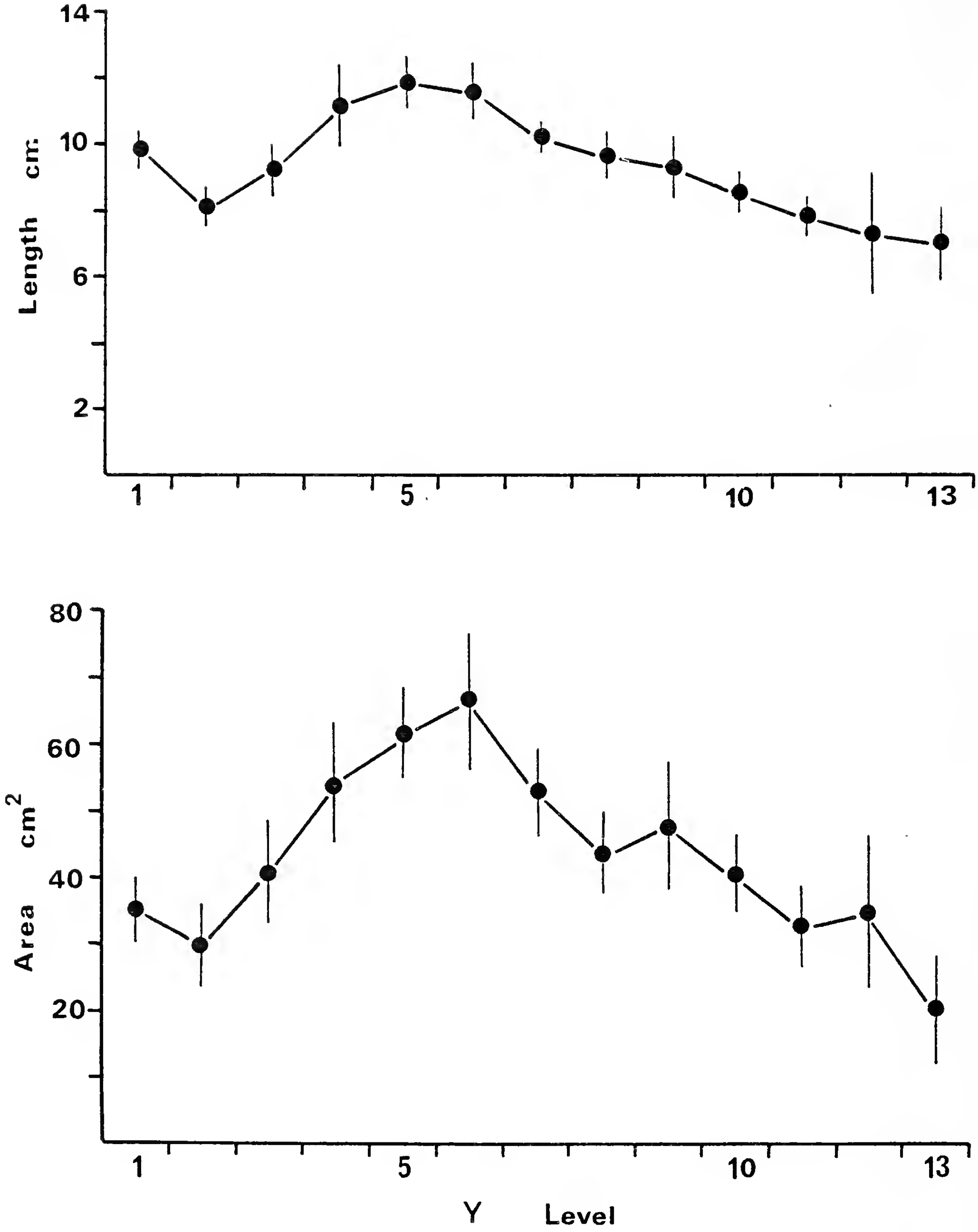

Figure 2

Variations in segment dimensions along the longest fronds of the 60 *Fucus* plants measured.

Vertical bars denote ± 1 Standard Error.

Table 4. Variations in segment length (and area)* along the longest fronds of *F. serratus* at the sites investigated

Plant level	Taynuilt	Kilmaronaig	Connel (Site 1)	Connel (Site 2)	Dunstaff. (shelter)	Dunstaff. (semi-exp)	Clachan (Site 1)	Clachan (Site 2)
1	8.3(14.9)	9.5(28.5)	11.8(42.5)	10.4(56.2)	9.7(25.2)	9.7(23.3)	11.1(44.4)	8.0(43.2)
2	6.1(12.2)	8.7(25.1)	10.7(53.5)	9.2(53.4)	7.0(15.4)	8.2(18.0)	7.7(24.6)	7.2(46.0)
3	6.9(17.9)	11.7(48.0)	12.2(75.6)	8.6(41.3)	7.5(13.5)	7.6(21.3)	9.4(47.0)	10.0(66.0)
4	7.9(25.3)	15.8(85.3)	14.5(81.2)	12.4(64.5)	8.3(18.3)	7.8(26.5)	12.2(58.6)	10.3(72.1)
5	9.6(32.6)	14.5(87.0)	12.9(85.1)	11.0(63.8)	10.9(50.1)	10.6(42.4)	10.4(56.2)	15.3(82.6)
6	10.2(34.7)	15.5(96.1)	11.8(61.4)	10.3(59.7)	9.4(45.1)	10.2(42.8)	14.9(125.2)	10.7(74.9)
7	9.3(22.3)	12.0(69.6)	9.9(43.6)	9.5(47.5)	9.5(53.2)	9.7(36.8)	11.6(81.2)	10.3(68.0)
8	9.2(27.6)	12.1(67.8)	12.0(31.2)	7.3(35.0)	9.6(48.0)	8.2(31.2)	11.5(62.1)	8.0(52.8)
9	8.8(28.2)	13.1(94.3)	8.0(35.2)	9.7(39.8)	8.9(49.8)	7.7(26.2)	12.3(86.1)	6.8(24.5)
10	6.2(16.2)	8.8(44.0)	8.5(25.2)	7.4(32.6)	9.1(52.8)	8.1(30.8)	11.3(61.0)	9.0(63.0)
11	6.6(21.1)	7.0(25.2)	-	8.0(26.4)	7.2(36.0)	7.0(26.6)	11.8(70.8)	7.0(28.0)
12	1.5(1.5)	14.0(84.0)	-	9.8(43.1)	6.3(26.5)	5.2(20.8)	7.8(39.0)	-
13	-	5.0(5.0)	-	-	7.3(30.7)	-	9.0(27.0)	-

* Values are cm and (cm^2)

Figure 2 and Table 4 examine the pattern of segment size along the main fronds of those plants which we examined. The pattern for length and area is broadly similar, both measures being maximal in the mid levels of the plants, and decreasing systematically towards the base of the plant and amongst the younger more distal dichotomies. The two most basal segments consist mainly of woody midrib and are therefore much more rod-like than the flatter segments of the main body of the plant. Analysis of variance again revealed systematic differences between the study areas, when the average size of segment faces for each plant, i.e. irrespective of their actual position along the plant, are considered ($F = 5.30$ for length, 7.14 for area, both at $P < 0.01$). Thus the absolute area available for colonisation varied not only between sites but also according to position along individual fronds. These results thus broadly agree with our earlier findings for *F. serratus* from the Menai Strait, north Wales (Wood and Seed 1980) and from Strangford Lough, Northern Ireland (Boaden *et al.* 1975; Seed *et al.* 1981).

The fauna and flora

1. The associated species. A total of 94 taxa (76 animal and 18 algal) was recorded from the 60 *F. serratus* plants examined. This figure, however, excludes several unidentified filamentous algae as well as the numerous meiofaunal taxa such as mites, nematodes, crustaceans, flatworms etc. These latter were common at all sites, especially amongst the hydroid and encrusting bryozoan colonies. The relative dominance of the major faunal groups is summarised in Figure 3. The fauna is almost equally composed of attached and vagile taxa, the former accounting for 60% of those represented.

2. The dominant species. Because most taxa were encountered only infrequently, most of our subsequent analyses have been restricted to the ten commonest species within this community. In order to qualify as 'common', a species must have occurred on at least 5% of the available segment faces at one or more sites. These comprised six bryozoans, *Flustrellidra hispida* (Fabricius), *Electra pilosa* (L.), *Alcyonidium hirsutum* (Fleming), *A. polyoum* Hassel, *Celleporella hyalina* (L.), and *Bowerbankia imbricata* (Adams), three hydroids *Dynamena pumila* (L.), *Campanularia flexuosa* (Hinks) and *Clava squamata* (Muller), and the serpulid *Spirorbis borealis* Daudin.

3. Distribution and abundance. Several measures of abundance of the dominant species are examined in Table 5 A-D, from which it will be seen that pronounced differences exist between the fauna at the eight study areas, even amongst the pairs of

virtually adjacent sites at Connel, Dunstaffnage and Clachan Sound. The ubiquity index indicates whether a particular site is suitable for colonisation, whereas the overall abundance of a species provides a measure of the relative suitability of that site. Abundance when present, on the other hand, shows how the abundance figure is made up; a species could, for example, have a generally low abundance or alternatively a relatively more restricted higher abundance. The extensive data presented in Table 5 are summarised in Table 6, in which a four point scale is used to indicate the relative abundance of each species.

The bryozoans *Flustrellidra* and *Alcyonidium*, the hydroid *Dynamena pumila* and the serpulid *Spirorbis borealis* were clearly the most prominent members of the *Fucus* community. *Flustrellidra* and *Alcyonidium* occasionally covered the entire surface of certain dichotomies, and in some cases *A. hirsutum* could be found growing away from the frond edge in finger-like protrusions. The maximum recorded abundance of *Dynamena* (90%) was only slightly lower than that of the bryozoans, whilst individual segment faces not infrequently supported several hundred spirorbids. *Dynamena* and *Spirorbis* were each maximally abundant at those sites where the other species was encountered only occasionally (Tables 5 and 6). *Flustrellidra* was abundant at four of the study sites and was common at a fifth site. *Electra* and *Alcyonidium* were both widely distributed, the latter rather surprisingly attaining its greatest abundance at Taynuilt, the innermost study site in Loch Etive (Figure 1), where the only other epifaunal associate amongst the dominant *F. serratus* epifauna was the hydroid *Campanularia*.

Overall abundance and ubiquity amongst the dominant species were generally well correlated (bottom line of Table 6). *Electra*, however, was an exception in this regard, since although one of the most ubiquitous species within the *Fucus* epifauna this opportunistic species generally only occurred at relatively low levels of abundance.

Table 7 summarises the correlations between the overall abundance of *Flustrellidra* and *Spirorbis*, and respectively the occurrence of ancestrulae or juveniles on the same plant. The statistically significant correlations expressed in this table indicate that recruitment broadly paralleled the distribution of established populations both between sites (for both species) and within sites (for *Flustrellidr*a).

4. Zonation of species along the fronds. The dominant taxa within the *F. serratus* epifauna are not distributed at random along the length of the plants but exhibit distinct 'preferences' for particular regions. This zonation is

Table 5A. Measures of abundance for the most common species in the fauna of *F. serratus*

Site Species	Units (1)	Plants (2)	Faces (3)	Ubiquity % (4)	Overall (5)	abundance When present (6)	Maximum (7)	Stem height (8) (mm)
Taynuilt:								
Alcyonidium spp.	%	10	135	66.2	22.1(2.0)	33.3(2.5)	100	-
Campanularia flexuosa	%	8	39	19.1	0.7(0.2)	4.9(0.7)	30	7.5(0.4)
Kilmaronaig:								
Alcyonidium spp.	%	10	58	29.6	4.0(0.8)	13.4(2.4)	65	-
Electra pilosa	%	9	94	48.0	5.1(0.6)	10.6(1.1)	50	-
Bowerbankia imbricata	P/A	8	36	18.4	---------- not recorded ----------			-
Spirorbis borealis adults	N	9	60	30.1	1.3(0.2)	4.3(0.6)	22	-
S. borealis juveniles	N	9	13	6.6	0.3(0.1)	4.7(1.4)	17	-
Campanularia flexuosa	%	10	127	64.8	6.9(0.7)	10.7(1.0)	40	10.3(1.0)
Clava squamata	P/A	10	43	21.9	---------- not recorded ----------			-
Dynamena pumila	%	10	105	53.6	6.3(0.7)	11.8(1.1)	50	11.6(0.4)

(1) Abundance scored as percentage cover (%), present or absent (P/A), or number of individuals present (N).
(2) Number of plants on which the species was recorded at least once.
(3) Number of faces on which the species was recorded at least once.
(4) Ubiquity index = 100 (number of faces with species present)/(number of faces examined).
(5) Mean abundance (±SE) per segment face over all faces examined.
(6) Mean abundance (±SE) on those segment faces colonised.
(7) Maximum abundance on any single segment face.
(8) Mean height (±SE) of longest upright stem.

Table 5B. Measures of abundance for the most common species in the fauna of *F. serratus*

Site Species	Units (1)	Plants (2)	Faces (3)	Ubiquity % (4)	abundance Overall (5)	 When present (6)	 Maximum (7)	Stem height (8) (mm)
Connel (Site 1):								
Alcyonidium spp.	%	5	44	55.0	8.0(1.6)	14.4(2.6)	70	-
Electra pilosa	%	5	34	42.5	2.7(0.6)	6.4(1.1)	25	-
Bowerbankia imbricata	P/A	5	14	17.5	----------	not recorded	----------	-
Flustrellidra hispida	%	5	47	58.8	14.2(2.4)	24.1(3.4)	80	-
Ancestrulae	N	5	51	63.8	8.4(1.3)	13.2(1.6)	57	-
Spirorbis borealis adults	N	5	54	67.5	9.3(1.4)	13.8(1.8)	66	-
S. borealis juveniles	N	5	61	76.3	36.5(5.1)	47.9(6.0)	192	-
Campanularia flexuosa	%	5	30	37.5	0.9(0.2)	2.4(0.5)	10	9.2(0.9)
Clava squamata	P/A	5	14	17.5	----------	not recorded	----------	-
Dynamena pumila	%	4	6	7.5	0.1(-)	1.0(-)	1	10.0(2.3)
Connel (Site 2):								
Alcyonidium spp.	%	4	31	33.0	6.9(1.6)	20.9(3.8)	80	-
Electra pilosa	%	5	44	46.8	6.1(1.3)	12.9(2.3)	50	-
Flustrellidra hispida	%	5	40	42.5	7.2(1.5)	17.0(3.0)	80	-
Ancestrulae	N	5	42	44.7	3.7(0.8)	8.3(1.4)	35	-
Spirorbis borealis adults	N	5	24	25.5	0.8(0.2)	3.1(0.7)	17	-
S. borealis juveniles	N	3	11	11.7	0.2(0.1)	2.1(0.3)	4	-
Campanularia flexuosa	%	5	61	65.0	4.8(0.8)	7.4(1.1)	50	10.1(0.7)
Clava squamata	P/A	5	43	45.7	----------	not recorded	----------	-
Dynamena pumila	%	5	54	57.5	16.1(2.4)	28.0(3.3)	90	18.1(0.9)

Table 5C. Measures of abundance for the most common species in the fauna of *F. serratus*

Site Species	Units (1)	Plants (2)	Faces (3)	Ubiquity % (4)	abundance Overall (5)	 When present (6)	 Maximum (7)	Stem height (8) (mm)
Dunstaffnage (shelter):								
Alcyonidium spp.	%	10	114	52.8	7.8(2.1)	11.6(1.8)	90	-
Electra pilosa	%	10	126	58.3	5.0(0.6)	9.9(1.8)	65	-
Flustrellidra hispida	%	5	12	5.6	0.4(0.2)	8.0(3.1)	35	-
Ancestrulae	N	10	87	40.3	1.4(0.2)	3.5(0.5)	28	-
Spirorbis borealis adults	N	10	142	65.7	10.3(1.4)	15.7(2.0)	212	-
S. borealis juveniles	N	10	186	86.1	31.9(3.2)	37.1(3.6)	242	-
Dynamena pumila	%	6	27	12.5	0.3(0.1)	2.6(0.8)	20	7.1(0.7)
Dunstaffnage (semi-exp):								
Alcyonidium spp.	%	10	93	54.7	6.3(1.1)	11.5(1.7)	80	-
Electra pilosa	%	10	117	68.0	4.3(0.6)	6.4(0.8)	35	-
Flustrellidra hispida	%	10	90	52.3	14.4(1.7)	27.6(2.6)	100	-
Ancestrulae	N	10	109	63.4	8.0(1.0)	12.6(1.4)	67	-
Dynamena pumila	%	10	49	28.5	2.5(0.5)	8.8(1.4)	40	11.0(0.6)

Table 5D. Measures of abundance for the most common species in the fauna of *F. serratus*

Site Species	Units (1)	Plants (2)	Faces (3)	Ubiquity % (4)	abundance Overall (5)	abundance When present (6)	abundance Maximum (7)	Stem height (8) (mm)
Clachan (Site 1):								
Alcyonidium spp.	%	5	11	10.6	0.4(0.2)	3.8(1.1)	10	-
Electra pilosa	%	4	31	29.8	1.5(0.3)	5.2(0.7)	15	-
Flustrellidra hispida	%	5	78	75.0	14.4(1.8)	19.2(2.2)	90	-
Ancestrulae	N	5	62	59.6	7.8(1.0)	18.1(2.1)	65	-
Celleporella hyalina	%	5	27	30.0	0.9(0.3)	3.4(0.9)	20	-
Spirorbis borealis adults	N	5	76	73.1	21.1(4.2)	28.8(5.5)	305	
S. borealis juveniles	N	5	91	87.5	90.0(11.3)	102.9(12.3)	512	-
Campanularia flexuosa	%	5	80	76.9	8.4(1.1)	10.9(1.3)	60	10.6(0.4)
Dynamena pumila	%	5	30	28.9	1.0(0.3)	3.4(0.9)	20	8.3(0.7)
Clachan (Site 2):								
Alcyonidium spp.	%	5	21	17.8	0.8(0.3)	4.4(1.1)	10	-
Electra pilosa	%	5	27	22.9	0.6(0.2)	2.6(0.8)	10	-
Flustrellidra hispida	%	5	67	56.8	12.1(2.2)	21.5(3.0)	70	-
Ancestrulae	N	5	61	51.7	7.2(1.9)	13.9(3.3)	81	-
Celleporella hyalina	%	5	19	16.1	0.5(0.2)	2.8(0.7)	5	-
Spirorbis borealis adults	N	5	34	28.8	1.0(0.4)	3.6(1.0)	16	-
S. borealis juveniles	N	5	49	41.5	3.1(1.0)	7.5(2.1)	43	-
Campanularia flexuosa	%	5	49	41.5	2.7(0.7)	6.5(1.5)	20	8.8(0.9)
Dynamena pumila	%	5	80	67.8	13.7(2.5)	20.4(3.2)	80	12.2(0.7)

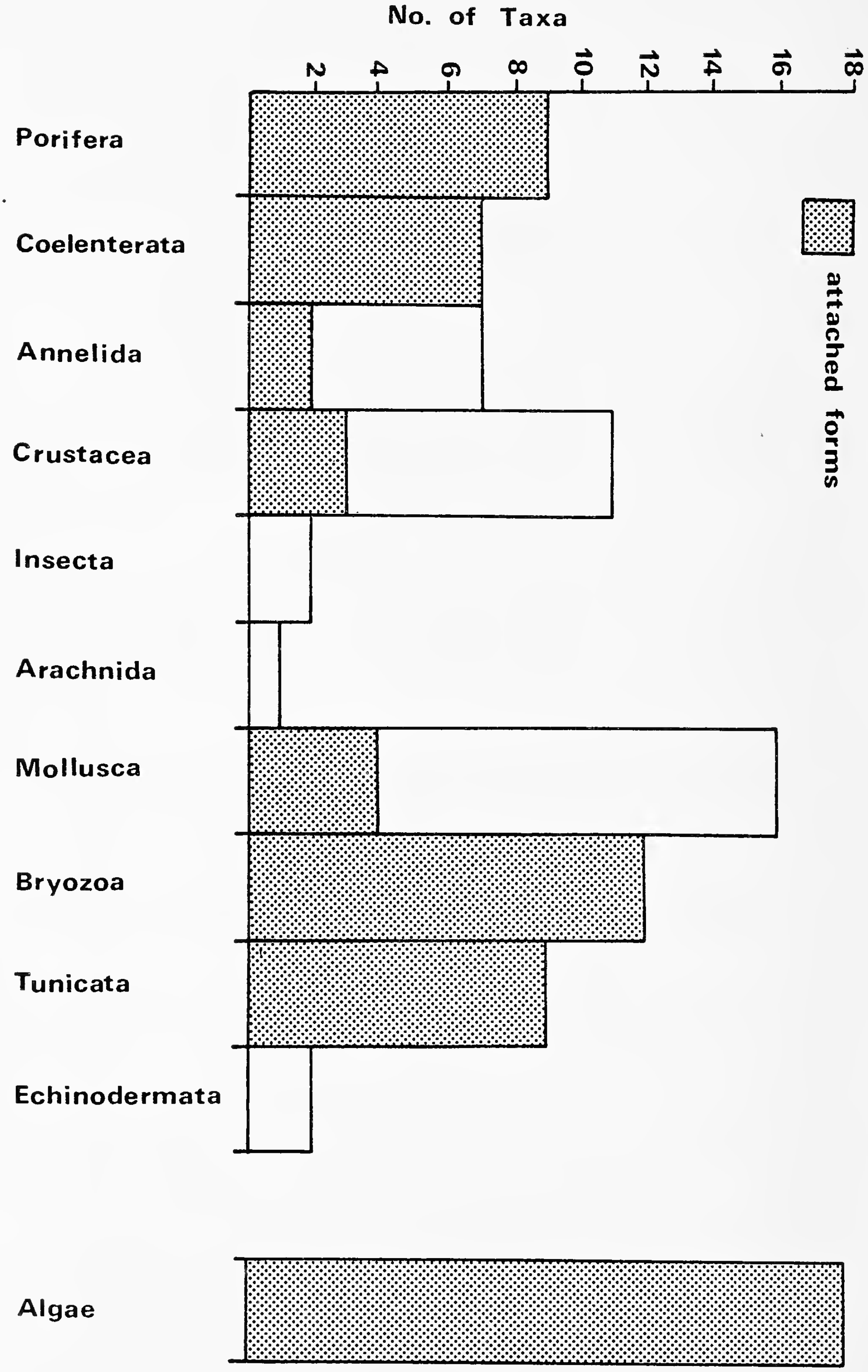

Figure 3

The relative dominance of the major faunal groups within the epifauna of *F. serratus*.

illustrated in Figures 4 and 5, in which both the ubiquity and intensity of colonisation are compared. *Flustrellidra* exhibited a marked propensity, especially in terms of its abundance, for basal dichotomies (Y1-Y4). *Electra* and *Alcyonidium* peaked in abundance further out along the fronds at Y levels 4-5 and 5-7 respectively, but were both noticeably less abundant on basal segments where *Flustrellidra* was most common. *Dynamena* and *Campanularia* were distributed over a relatively wide range of segment faces, but the abundance of both these hydroids declined steeply beyond Y levels 6 and 7. The established population of *Spirorbis* occurred mainly in the bushier central regions of the plants, and although the juvenile stages of this species exhibited a similar pattern of distribution, these peaked in abundance somewhat further out along the fronds (Y6-Y8). *Flustrellidra* ancestrulae were fairly ubiquitous with regard to their distribution along the fronds, but were most abundant on segments Y5-Y10. This latter is especially noteworthy in view of the more basal distribution of adult colonies.

When the abundance of a species on plants which vary in their number of dichotomies is averaged according to Y levels, as in Figures 4 and 5, the relatively sharp zonation patterns which may characterise individual fronds frequently become slightly blurred. This effect is more pronounced amongst those organisms with a more distal distribution if, as in this investigation, Y levels are ordered sequentially from the base of the plant. We have therefore re-examined the distribution of *Flustrellidra* and *Spirorbis* along the longest fronds when these are subdivided into ten segments of equal length (Figure 6); this transformation of our original data was possible since the size of each Y level is known. In this way the *relative* position of each segment remains constant, irrespective of any differences in overall plant length. In Figure 6 the more distal distributions of juvenile spirorbids, and even more especially *Flustrellidra* ancestrulae, are clearly indicated.

5. Preferences for concave or convex surfaces. Beyond the most basal segments the fronds of most *Fucus* plants have a recognisable concave face, and all but *Dynamena* showed a slight tendency to settle on this face rather than on the obverse (Table 8). Only in the case of *Campanularia*, however, was this difference statistically significant ($\chi^2 = 8.48$, $p < 0.01$), and when actual abundances on the colonised faces were considered, *Flustrellidra* (and its ancestrulae), *Spirorbis*, *Campanularia* and *Celleporella* were all significantly more numerous on concave segment faces. The erect stems of *Campanularia* were also slightly, although consistently, taller on concave (7.1 ± 0.7 SE mm) than on convex (6.4 ± 0.7) surfaces ($p < 0.01$,

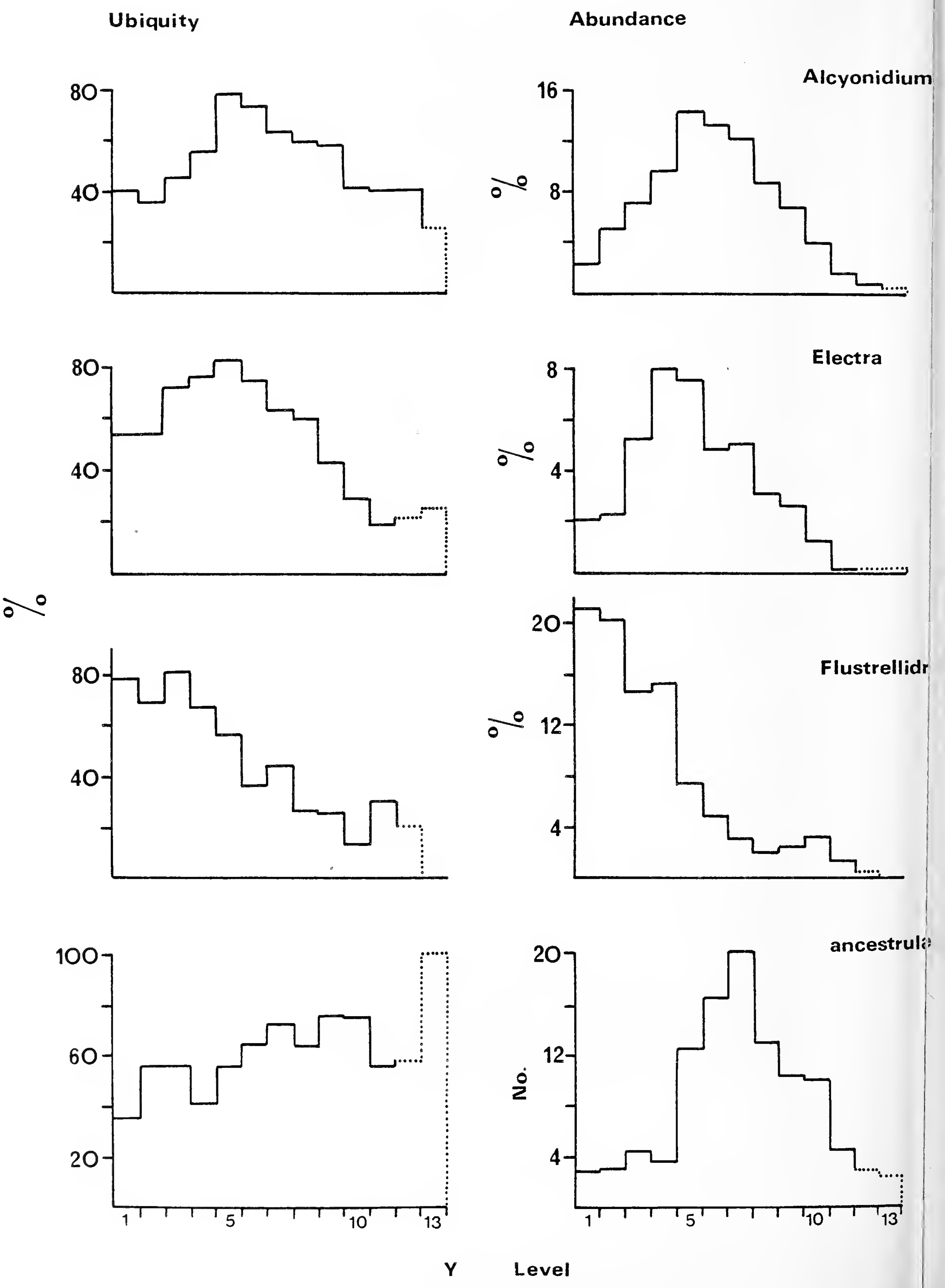
Ubiquity
Abundance
Alcyonidium
Electra
Flustrellidr
ancestrul
%
%
%
%
No.
80
40
80
40
80
40
100
60
20
16
8
8
4
20
12
4
20
12
4
1
5
10
13
1
5
10
13
Y
Level

Figure 4

Ubiquity and overall abundance of the common species at different plant levels.

Ubiquity calculated as % of available segment faces colonised, abundance as % cover (except for ancestrulae, which were counted). Results based on species present on less than 10 segment faces are indicated by broken lines. Only those plants on which the species was present are included.

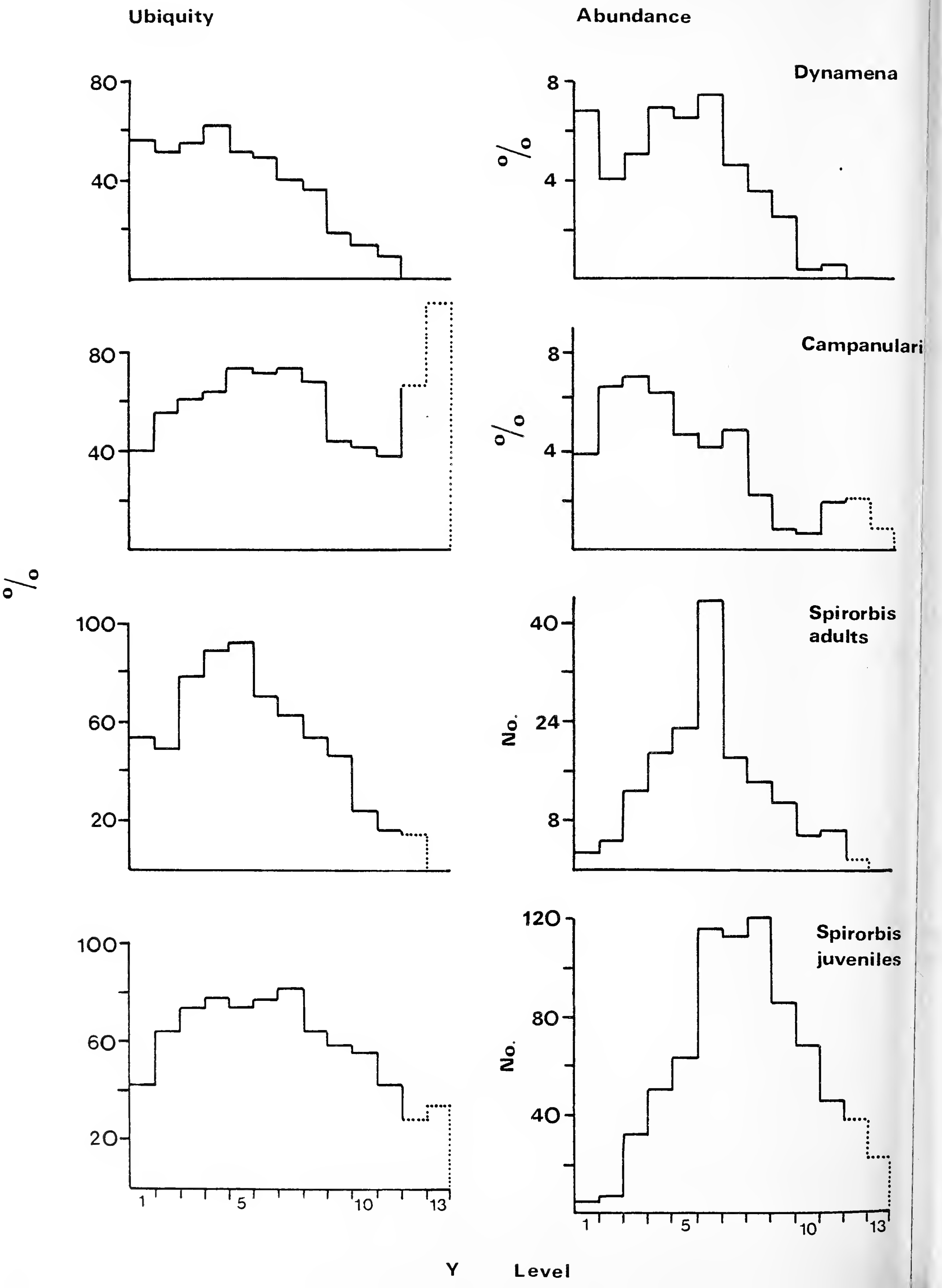
Ubiquity
Abundance
Dynamena
Campanulari
Spirorbis adults
Spirorbis juveniles
%
No.
80
40
100
60
20
8
4
40
24
8
120
80
40
1
5
10
13
Y Level

Figure 5

Ubiquity and overall abundance of the common species at different plant levels.

Ubiquity calculated as % of available segment faces colonised, abundance as % cover (except for spirorbids, which were counted). Results based on species present on less than 10 segment faces are indicated by broken lines. Only those plants on which the species was present are included.

Wilcoxon Matched Pairs Signed Ranks Test). The stems of *Dynamena*, on the other hand, showed no systematic trend between concave or convex surfaces (10.9 ± 0.7 and 10.8 ± 0.7 SE mm respectively, $p > 0.05$).

The overall propensity for concave surfaces, shown by the majority of the dominant species within the *Fucus* epifauna, is broadly maintained at most of those sites at which the species is adequately represented (Table 9). At Connel, however, *Electra* was slightly, although consistently, more abundant on convex surfaces.

6. Species diversity. The mean number of species present on the longest fronds of *F. serratus* varied from a minimum of 4.6 ± 0.6 SE at Taynuilt to a maximum of 20.8 ± 2.4 in the evidently more favourable conditions at Clachan Sound (Table 10). These differences could simply reflect intersite variation in the overall size of plants. However, since the number of species along the main frond is highly correlated with the number present on each segment face ($r_s = 0.923$, $P < 0.01$) there still remains a four-fold difference between sites, even when species counts are expressed in units of a single dichotomy. We have used species counts as a simple measure of taxonomic diversity in view of the inherent difficulties in reconciling organisms with different growth forms (e.g. solitary and colonial species) within a single diversity index.

Analysis of species diversity in relation to plant variables showed no systematic pattern in respect of either plant length or structural diversity, except at the sheltered Dunstaffnage site where length and diversity were negatively correlated ($r_s = -0.655$; $P < 0.05$), i.e. indicating that the longer plants tended to be significantly less diverse than shorter plants at this particular site. At Taynuilt and the semi-exposed Dunstaffnage site, on the other hand, diversity was positively correlated with branching index ($r_s = 0.694$ and 0.796 respectively, both at $P < 0.05$), indicating a greater diversity amongst the more highly branched plants. Moreover, diversity and branching index are also significantly correlated ($r_s = 0.738$; $p < 0.05$) when the average values of these variables at all eight sampling sites are considered (Table 10). This latter, however, has perhaps relatively little biological significance since factors other than plant structure could here be responsible for differences in faunal diversity.

DISCUSSION

The fronds of *F. serratus* clearly provide a suitable attachment surface for numerous sedentary taxa, as evidenced by

Table 6. Relative abundance of the most common species in the fauna of *F. serratus*.

Abundance recorded as: A abundant; C common; O occasional; R rare or absent.

Site Species	*Alcyonidium*	*Electra*	*Flustrellidra*	Ancestrulae	*Dynamena*	*Spirorbis* (Ad)	*Spirorbis* (Juv)	*Campanularia*	*Clava*	*Celleporella*	*Bowerbankia*
Taynuilt	A	R	R	R	R	R	R	O	R	R	R
Kilmaronaig	C	C	R	R	C	O	O	C	O	R	O
Connel (Site 1)	C	C	A	C	O	C	A	O	O	R	O
Connel (Site 2)	C	C	C	O	A	O	O	C	O	R	R
Dunstaffnage (shelter)	C	C	O	O	O	A	A	R	R	R	R
Dunstaffnage (semi-exp)	C	C	A	C	O	R	R	R	R	R	R
Clachan (Site 1)	O	O	A	C	O	A	A	C	R	O	R
Clachan (Site 2)	O	O	A	C	A	O	O	C	R	O	R
Max. abundance (1)	22%	6%	14%	8	16%	21	90	8%	not quantified		
P (2)	**	NS	*	**	**	*	*	*	†	†	†

(1) Maximum average abundance per segment face at any site.

(2) Significance levels associated with Spearman Rank Order Correlations (see text for details).

* $p < 0.05$; ** $p < 0.01$; NS not significant; † too few data.

Table 7. Spearman Rank Order Correlations between overall abundance and recruitment on to the same plants

* p ≦ 0.05; ** p < 0.01; NS not significant; † absent or too few data.

Site	*Flustrellidra*	*Spirorbis*
Taynuilt	†	†
Kilmaronaig	†	NS
Connel (Site 1)	0.667* (1)	NS
Connel (Site 2)		†
Dunstaffnage (shelter)	0.733*	NS
Dunstaffnage (semi-exp.)	0.667*	†
Clachan (Site 1)	0.890**(1)	NS
Clachan (Site 2)		†
Between sites (2)	0.950**	0.886*

(1) Sites similar, therefore data pooled.
(2) Based on site averages.

the diverse nature of their epifaunal communities. This apparent preference for this fucoid cannot be due entirely to its low intertidal or shallow subtidal position, since the blades of laminarians support relatively impoverished faunas (Seed and Harris 1980), yet these algae experience even less desiccation than *F. serratus*. The epifauna of the Serrated Wrack on the Argyll coast is dominated by bryozoans, hydroids and serpulids. Whilst the structure of this community is thus similar to those described for *F. serratus* elsewhere (Boaden *et al.* 1975; Seed and O'Connor 1981b; Stebbing 1973; Wood and Seed 1980), some species differences do exist and it appears, therefore, that *Fucus* may provide an array of resources which can be occupied in different areas by ecologically equivalent species.

Although we have no quantitative data regarding the physical conditions prevailing at our sample areas, it seems clear from our observations that environmental factors are dominant sources of variation in species abundance. In our earlier studies of *F. serratus* samples from Strangford Lough we found marked differences between species as to their environmental preferenda (Boaden *et al.* 1975, 1976; O'Connor *et al.* 1979, 1980), so it is perhaps not too surprising that the Argyll community should be similarly regulated. Most of the sedentary filter feeding taxa in the Strangford Lough community attained their maximum abundance at sites experiencing a high degree of water flow and turbulence but a low silt loading, although certain species, e.g. *Spirorbis*, the bryozoan *Membranipora* and the tunicate *Polyclinum*, were evidently more tolerant of sediment and were most abundant in quieter, more turbid conditions. Doyle (1975) has demonstrated that excessive turbulence can be a major source of mortality in serpulids. We suspect that reduced salinities in the upper reaches of Loch Etive at Taynuilt, and moderate wave action at the semi-exposed Dunstaffnage site, may account, at least in part, for the less diverse fauna at these sites, for the *Fucus* plants were themselves less developed there than at other sites (Table 3).

Plant size and structure afford attached species a range of microenvironments by alleviating the severity of their physical surroundings. Ott (1967), for example, found that water currents at the centre of *Cystoseira* plants were only a fifth of those at the periphery, while Seed *et al.* (1981) demonstrated that the structure of *F. serratus* had a pronounced influence on the pattern of water flow through individual plants. Clearly, therefore, small *Fucus* plants would not offer this type of environmental amelioration to the same extent as would the larger plants. The large *Fucus* plants at Clachan Sound supported a particularly diverse epifaunal community and

Table 8. Utilization of concave and convex surfaces of *F. serratus* by the common species

* $p < 0.05$; ** $p < 0.01$; NS not significant.

Species	Units (1)	Faces (2)	Percentage of faces colonised that were		Mean abundance (±SE) when present on faces that were		P (3)
			(a) concave	(b) convex	(a) concave	(b) convex	
Alcyonidium spp.	%	507	54	46	18.8(1.9)	17.7(1.9)	NS
Electra pilosa	%	473	52	48	8.6(0.7)	7.7(0.8)	NS
Flustrellidra hispida	%	334	50	50	23.4(2.1)	21.0(1.9)	*
Ancestrulae	N	412	52	48	11.5(1.6)	7.5(0.8)	**
Dynamena pumila	%	351	49	51	12.9(1.4)	13.8(1.7)	NS
Spirorbis borealis (adults)	N	390	53	47	16.2(2.4)	13.7(1.8)	*
S. borealis (juveniles)	N	359	51	49	51.8(6.7)	51.1(7.9)	NS
Campanularia flexuosa	%	386	58	42	9.2(1.1)	7.5(0.9)	**
Clava squamata	P/A	100	54	46	---------- not recorded ----------		
Celleporella hyalina	%	46	51	49	4.4(0.3)	2.2(0.1)	**
Bowerbankia imbricata	P/A	50	54	46	---------- not recorded ----------		

(1) Abundance scored as percentage cover (%), present or absent (P/A), or number of individuals present (N).
(2) Number of faces on which the species was recorded at least once (maximum 1184).
(3) Wilcoxon Matched Pairs Signed Ranks test based on plant averages.

Table 9. Utilization of concave surfaces of *F. serratus* by the common species at the sites investigated

Species	Taynuilt	Kilmaronaig	Connel 1+2	Dunstaffnage (shelter)	Dunstaffnage (semi-exposed)	Clachan 1+2
Alcyonidium spp.	**	NS	NS	*	NS	†
Electra pilosa	†	NS	[**]	NS	*	†
Flustrellidra hispida	†	†	NS	†	*	*
Ancestrulae	†	†	*	*	**	†
Dynamena pumila	†	NS	NS	†	NS	NS
Spirorbis borealis (adults)	†	NS	NS	**	†	NS
S. borealis (juveniles)	†	NS	†	**	†	NS
Campanularia flexuosa	†	*	*	†	†	†

Wilcoxon Matched Pairs Signed Ranks test:

* $p < 0.05$; ** $p < 0.01$; NS not significant; † species absent or too few data.

1+2 Pooled data for Sites 1 and 2.

[ ] Brackets indicate preference for convex surface.

Table 10. The relationship between faunal diversity and plant structure

Site	Mean (±SE) No. of species per		Correlation (1) between No. spp./dichotomy and		
	Frond	Dichotomy	Plant length	Branching index	H/H max
Taynuilt	4.6(0.6)	0.47(0.07)	NS	0.694*	NS
Kilmaronaig	11.3(0.8)	1.19(0.09)	NS	NS	NS
Connel (Site 1)	13.8(1.9)	1.73(0.20)	NS	NS	NS
Connel (Site 2)	14.0(1.0)	1.60(0.25)	NS	NS	NS
Dunstaffnage (shelter)	6.6(0.7)	0.63(0.07)	-0.655*	NS	NS
Dunstaffnage (semi-exp)	6.6(0.5)	0.78(0.06)	NS	0.796*	NS
Clachan (Site 1)	20.8(2.4)	2.08(0.37)	NS	NS	NS
Clachan (Site 2)	15.0(0.6)	1.63(0.13)	NS	NS	NS
Between sites			NS	0.738*	NS

(1) Spearman Rank Order Correlations : * $p < 0.05$; ** $p < 0.01$; NS not significant.

in this regard were similar to tidal rapid faunas elsewhere (Kitching and Ebling 1967; Ryland and Nelson-Smith 1975).

Physical factors, either directly or via their influence on plant growth, may not always be responsible for intersite differences in species abundance - biotic factors such as competition and predation may effectively exclude species from their 'preferred' sites. *Spirorbis* and *Electra* are often overgrown by encrusting species (O'Connor and Lamont 1978; Stebbing 1973; Wood and Seed 1980). These species reduce the effects of competition by utilization of sites normally avoided by major competitors, by being relatively less specific in their choice of substrata, or by settling on and/or growing towards the younger less heavily encrusted regions of the plants. Although *Spirorbis* can redirect its growth in an attempt to elevate the tube orifice above the competing species, most individuals are ultimately smothered. Such observations confirm Jackson's (1977) assertion that colonial species generally out-compete solitary species. Although the ability of hydroid colonies to develop vertically may reduce the impact of overgrowth by adherent forms, some species can evidently withstand high bryozoan densities far better than others (Seed *et al.* 1983). Species like *Dynamena* develop an extended stoloniferous network with simultaneous growth in lateral and vertical planes. Once these stolons are overgrown they are presumably hindered in their function of nutrient transport, and individual zooids or even complete stems can be lost.

A species may be absent from any given site either because conditions are unsuitable for adult growth and survival, or because larvae, for whatever reason, fail to settle there. Thus at Taynuilt and Kilmaronaig only ten *Flustrellidra* ancestrulae were recorded on the twenty plants (400 segment faces) which we examined, despite the relative abundance of this bryozoan elsewhere in Loch Etive (Tables 5 and 6). The relative failure of *Flustrellidra* to colonise *Fucus* plants at the sheltered Dunstaffnage site is perhaps even more remarkable, in view of its success at the adjacent semi-exposed site. At Connel, Dunstaffnage and Clachan, recruitment and/or survival of *Spirorbis* is also exceedingly localised, again resulting in a very patchy distribution. These results suggest that the short-lived (several hours) larvae of *Flustrellidra* and *Spirorbis* may have extremely limited powers of dispersal. In Table 7 the occurrence of established and newly recruited populations of these two species on the same plant is examined. Although the between-site correlations were statistically significant for both species, these are perhaps of little biological significance since one would intuitively expect

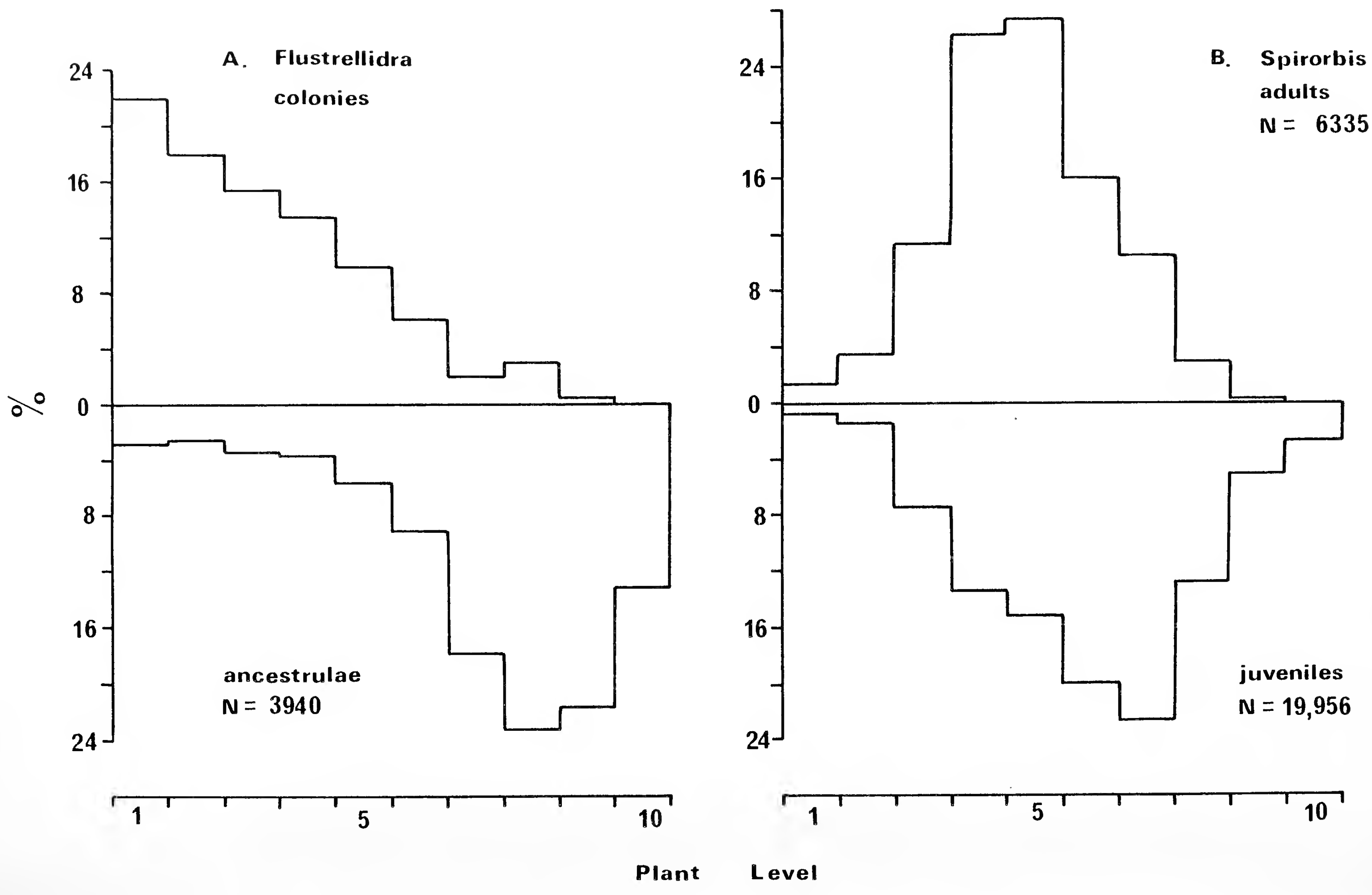

Figure 6. Abundance of A) *Flustrellidra* and B) *Spirorbis* along *F. serratus* when each plant is divided into 10 segments of equal length irrespective of plant size.

heavier settlements at those sites where the species is already well established. The significant within-site correlations in the case of *Flustrellidra*, on the other hand, suggest either that the larvae are highly gregarious or that the majority of them are 'retained' within the body of the plant on which they had been released (assuming that the number of larvae actually released is proportional to the abundance of established colonies). Either explanation would at least partially account for the very patchy distributions which characterise several of the dominant species within the *Fucus* epifauna both here and elsewhere.

The major species within the *Fucus* epifauna occur in more or less well defined zones along the plants. Fucoid algae grow by apical meristems and their fronds constitute an age gradient in which the newly grown segments are distal. Zonation along such fronds can be established by differential larval settlement on to the youngest segment faces which carry fewer established colonies, a strategy which is clearly adaptive in a space limited system. This has been established for various species, in some cases associated with oriented growth towards the growing edges of the frond (Ryland and Stebbing 1971; Wood and Seed 1980), and was apparently the case with *Flustrellidra* in our (June) sample (Figure 6). Buss (1979) considers that habitat selection and directional growth are the main mechanisms evolved in marine invertebrates for locating spatial refuges. Since individuals within these refuges will presumably contribute more to future generations by virtue of their higher survival, selection might be expected to favour mechanisms for exploiting such refugia.

Zonation can also be due to differential survival in different microenvironments along the fronds. At higher intertidal levels, where dessication is presumably more extreme, *Alcyonidium hirsutum* occurs further out in the bushier parts of *Fucus* (Wood and Seed 1980). O'Connor and Lamont (1978) similarly related *Spirorbis* distribution within *Fucus* plants to the risk of dessication. However, we have also found evidence of epifaunal species altering their zonation patterns in the presence of major competitors, so zonation need not be determined exclusively by environmental considerations (Boaden *et al.* 1976; O'Connor *et al.* 1980).

F. serratus fronds are partially folded, thereby producing clearly recognizable concave and convex surfaces. Settlement is preferentially onto the concave surfaces in some species, e.g. *Alcyonidium*, *Spirorbis* and *Flustrellidra* (Wood and Seed 1980; Wisely 1960; this study) is more pronounced in the upper shore levels, possibly because concave surfaces more readily retain a film of water which prevents dessication (Wood and Seed 1980), and may be linked to competitive interactions (Boaden *et al.* 1976). However, the possibility that established populations may obtain some degree of local protection from currents or the abrasive effects of adjacent fronds cannot be dismissed. Moreover, local eddying around the frond edges could also be instrumental in providing generally more favourable feeding conditions on concave surfaces.

Two major shortcomings of our study are recognised: the lack of quantitative data regarding the physical conditions at the study sites, and the temporally restricted nature of the sampling programme. Although detailed distributions of species are known to vary seasonally (Seed *et al.* 1981), the patterns of spatial segregation which emerged in our present study (June) were remarkably similar to those which we have previously described amongst the *F. serratus* epifauna in the Menai Strait (October-March) and Strangford Lough (March-April). Taken overall, our results indicate that the common sessile taxa which are potential space competitors within the *F. serratus* epifauna can probably achieve some degree of ecological isolation, via their differential use of sites located in different physical and biological environments, and by their differential use of microenvironments provided within single plants.

SUMMARY

The epifaunal community associated with the fronds of *Fucus serratus* at eight physically and biologically contrasted sites along the Argyll coast was studied in June 1977. The 60 plants which we examined in detail yielded a total of 76 macrofaunal and 18 macroalgal taxa. Many of these taxa, however, were encountered only infrequently, and most of our analyses were accordingly restricted to the ten most common species - these comprised six bryozoans, three hydroids and one serpulid. The distribution and abundance of the dominant fauna, and the size and structure of the *Fucus* plants themselves, showed significant intersite variation even on a very localised scale. Species were not randomly distributed along individual fronds but occupied distinct zones within the plants. Most species were generally more prolific on the concave surfaces of the plants, and the bryozoan *Flustrellidra hispida* settled in greater profusion on this face than on the obverse. The correlation between faunal diversity and plant structure was weak and probably of limited biological significance. Differential distribution of the dominant encrusting fauna

within this *Fucus* community results in a considerable degree of niche segregation and ecological isolation.

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SOME OBSERVATIONS ON THE FLOCKING AND FORAGING BEHAVIOUR OF RAVENS AT DRIMNIN, ARGYLL

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Flocking Behaviour

Flocks of scavenging Ravens *Corvus corax* have been recorded at historic battlefields, and were even encouraged for their sanitation value around mediaeval towns, but the cause of flocking has long been in dispute, the importance of food as a basic stimulus being variously questioned (e.g. Bannerman and Lodge 1953, Coombes 1948).

Flocking can occur at any time of the year, but was seasonal in the present study on the Drimnin Estate, which comprises some 7,000 acres of wet heather moorland lying at the north-western tip of the Morvern peninsula. During the breeding season, from late February onwards, Ravens were only noted in ones and twos, until the appearance in June-July of family groups comprising six birds in 1977 and five birds in 1978, while a flock of eleven birds in July 1978 perhaps represented two family parties on neutral ground between adjoining territories.

During September to mid-October 1977 a conspicuous flock of over 30 Ravens was scavenging the carcases of some 25 lambs which had died, probably mainly from louping-ill virus, in the pre-sales gathering parks; a large flock also occurred at this time in 1978, but scavenging was much less spectacular since inoculation had apparently been much more effective, and only ten lamb carcases were available to this flock of 20 birds. These large flocks apparently partially disbanded after the autumn lamb-mortality peak, although smaller November flocks of around ten birds occurred in both years, e.g. at the Amphitheatre grallochs in 1978. Numbers could also build up again sporadically before nesting re-commenced, as with 14 birds in January 1978, and the 25 birds in February 1979 scavenging a Red Deer hind which was the only fresh carcase available on the Estate during exceptionally severe snowfalls over a three-week period (Hancox 1979).

Flocking at Drimnin, at any rate, therefore occurred during the non-breeding season, and apparently included birds from within a radius of some five miles, i.e. from Mull, Ardnamurchan, and the Barr-Fiunary forest. The Ravens in these flocks often indulged in soaring social aerobatic displays on ridge thermals, frequently participating as pairs. It seems probable that this annual semi-nomadic association of an immature or otherwise non-breeding mostly surplus population may be the fundamental basis of flocking, and may also be the derivation of pair formation in Ravens (Coombes 1948, Hewson 1957, Mylne 1961, M.G. Ridpath 1953 - quoted in Murton 1971). Non-breeding flocks, together with such interrelated ecological similarities as delayed maturity and high first-year mortality, also occur in Hooded Crows *Corvus corone* and other corvid species elsewhere in the world (Houston 1977, Rowley 1970).

Flocking may therefore be fundamentally socially induced but the attraction of a rich food source can undoubtedly be an over-riding or re-inforcing factor, as in the 20-30 strong Drimnin gatherings, congregations at rubbish dumps, some 150 birds at a knacker's yard in Wales (Mylne 1961), and flocks of up to 800 Ravens at stranded whales in the Hebrides and Shetlands (Baxter and Rintoul 1953). Nomadic flocking seems to be particularly prevalent on the Islands, and is well adapted to opportunistic feeding, since many of the smaller islands are only stocked with sheep seasonally.

Finally, some of the winter flocks seen in the Hebrides and the north of Scotland may be due to migration from Scandinavia (Bannerman and Lodge 1953, Coombes 1948), whereas gregarious communal roosts of up to 276 birds recorded from Wales, the Lakes, and Scotland are probably a corollary rather than a causal factor of flocking behaviour (Bannerman and Lodge 1953, Coombes 1948, Mylne 1961).

Foraging Behaviour

Sheep carrion constitutes a major element in Raven diet studies, and is probably a critical factor influencing territory size, breeding density, and nesting success, although early nesting ensures that young are reared during the period of maximum availability of both sheep and deer carrion (Coombes 1948, Marquiss *et al.* 1978, Murton 1971).

Spectacular carrion feeding was seen on several occasions at Drimnin. During September and October 1977 the 30-strong flock of Ravens was largely responsible for the scavenging from some 25 lamb carcases, each carcase yielding between 10kg and 15kg of meat and viscera and being gutted in under two weeks. This total of some 250-375kg of carrion potentially represented the overall food requirements of the flock during this period of six weeks, assuming a daily intake of some 200g per individual, i.e. a total of 6kg a day for the flock, since a Hooded Crow needs at least 70g a day and a Golden Eagle *Aquila chrysaetos* 250g (Houston 1977).

Similarly, during a short period in June 1978 the family party of five Ravens probably subsisted largely on two lamb carcases, successively gutting each of them of 3-4kg of carrion over a total of six days. During February 1979 the carcase of a young hind was gutted in under four days, but the 20-25kg of carrion consumed was shared amongst 25 Ravens, ten Hooded Crows and two Golden Eagles (Hancox 1979).

Raven 'predation', amounting to well under 1% of either the lamb crop or ewe stock in most studies, almost invariably affects non-viable individuals moribund due to other causes, and with regard to lambs has been attributed specifically to non-breeding bird flocks, both in Britain and Australia (Murton 1971, Rowley 1970). Very few clear instances of Raven pre-mortem 'attack' were noted at Drimnin, but three 1978 lambs involved either the June family party or the September flock. In contrast to this, however, Raven 'attacks' on ewes were in several cases related to parturient difficulties during the period when Raven flocks were not evident on the Estate, and in one of these cases, in early April, territorial resident birds were believed to be ferrying carrion from the ewe and a nearby deer carcase to nestlings.

Diagnostic criteria for sheep autopsies have been discussed by Houston (1977) and Rowley (1970), and although no criteria were cited as specific to Ravens, removal of the tongue via a neat hole in the floor of the mouth in sheep/lamb and deer carcases was regularly associated with Ravens at Drimnin, and was probably beyond the capabilities of Hooded Crows, which feed via the side of the mouth. Similarly, probably only powerful birds such as Ravens, Great Black-backed Gulls *Larus marinus* or Golden Eagles were able to evert limbs by retracting the limb bones like the fingers of a glove, to break bone fragments from scapulae and ribs (bone fragments often occurred in Raven pellets) or to extract unborn lambs from ewe carcases via the vent or groin.

Some additional observations on bird scavenging and predation at Drimnin are discussed elsewhere (Hancox 1979, Hewson 1984).

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THE AILSA CRAIG GANNET CENSUS, 1983-1984

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As in previous years, the Ailsa Craig Gannet census during 1983 and 1984 each took the form of a one-day census made from the sea in early May, with the usual check counts of selected control areas later in the year. After extensive tests over many years (see previous *Clyde Seabird Reports*) it became clear that the one-day census from the sea, combined with the later control counts, gave results strictly comparable with the original method of the census spread over an entire week, and this has been the method used for the past fourteen years, with the proviso that if any obvious discrepancy were to be found with the later control counts, then the entire census would be repeated. So far I am relieved to say that this has not happened.

Present Population

The detailed counts for 1983 and 1984 are given in Table 1, along with the comparative counts for the previous two years. As before, all are direct counts through binoculars of occupied nests, and all figures comprise the mean of several counts of each cliff-section, made at different times throughout the same day from the same counting-stations. Control counts made later in the year are used only as checks, and are not included in the official census.

The counts of 18,983 occupied nests in 1981, 20,161 occupied nests in 1982, 21,072 occupied nests in 1983, and 21,997 occupied nests in 1984 have each been the highest populations ever recorded for Ailsa. In 1982 the colony passed 20,000 occupied nests for the first time, and it is worth noting that up to 1950 the colony had shown an average population of only some 5,000 nests.

After the 1982 census, the results of another count of the 1982 Ailsa Gannets appeared (S. Murray and S. Wanless, *Scot. Birds,* 12: 225-226). This was based on a count made from photographs of the cliffs taken in July 1982, and gave a mean of 20,843 occupied sites. Although this was gratifyingly close to the actual census result of 20,161 occupied nests, especially since the authors were obviously quite unaware of all the annual counts published during the immediately

Table 1

Counts of Gannet Nests on Ailsa Craig
1981 - 1984

Total for each cliff section represents the mean
of several separate counts

Colony	1981	1982	1983	1984
Sliddery	287	290	299	348
Sliddery, Top Ridge	501	499	483	506
North of the Slunk	490	487	417	501
Foot of the Slunk	511	523	556	597
Above Ashydoo	240	239	244	287
Balvaar	902	999	1013	1037
Below Balvaar	171	198	283	308
Balvaar, Top Ridge	327	301	387	401
Balvaar to Cairn	463	502	544	549
The Cairn	2302	2499	2681	2703
Cairn to Mare	670	663	672	688
Barrheads	2194	2243	2301	2457
Above Black Holes	362	402	388	413
Mare	4107	4272	4101	4306
Mare, Lower Ledge	169	183	197	188
Above Bed o' Grass	221	247	288	303
Mare-Stranny Point, S1	484	573	568	596
Mare-Stranny Point, S2	490	551	592	614
Mare-Stranny Point, S3	722	751	787	841
Mare-Stranny Point, S4	791	848	889	942
Stranny Point, South Side	44	42	51	48
Main Craigs, Main Part	898	1024	1281	1303
Main Craigs, Top	1168	1287	1464	1499
Main Craigs, East	321	387	428	426
Main Craigs, East Top	90	88	96	89
Main Craigs, Far East	-	-	-	-
Main Craigs, Far East Top	58	63	62	47
Grand Total:	18983	20161	21072	21997

preceding years, this close correlation might have been partly fortuitous, and it could be unwise to assume too much too soon, since previous attempts at photographic counts, at least on Ailsa Craig, had been shown to be unreliable (see *Clyde Seabird Report,* 1: 6-7). It may be, of course, that advances in photographic counting techniques over the years have overcome previous disadvantages, so any future counts made by this method will be examined with cautious interest. In the meantime, however, it provides useful confirmation.

On at least four occasions during some 45 years of direct counts since 1936, the Ailsa colony has shown dramatic, and as yet unexplained, peaks and crashes of population, in 1940/41, 1955/56, 1960/61 and 1974/75, but no further 'crashes' have been recorded since 1975. Indeed, as previously reported, during the nine years from 1976 to 1984 the colony has steadily increased by approximately 1,000 nests a year.

Index of Room

An index of the amount of 'room' available for Gannets on Ailsa, arrived at by adding together the maximum number of nests ever counted on each individual section of the cliffs, had reached 19,643 nests by 1979 and 20,789 nests by 1981, but since the Gannets have now shown clear signs of moving back from the cliffs to colonise the sloping ground at the cliff tops, a tendency first noted in 1974 (a year of very marked increases) and now firmly established, the index of room is now largely academic, and is no longer a direct indication of the real space available for the expanding colony. Clearly, if the Gannets continue to utilise the sloping ground at the top of the cliffs, there is virtually no limit to the size of the population which the island can hold. Nevertheless, during twenty-five years the 'cliff' index actually doubled, from some 10,000 nests in 1955 to some 20,000 nests in 1980.

Previous Work

Direct counts of all occupied nests have now been carried out at the Ailsa Craig Gannet colony for nearly half a century. This work commenced in 1936, with a pioneer count by H.G. Vevers and James Fisher, and apart from a slight gap during the war years, when only curtailed counts and estimates of population could be used, they have continued without a break ever since.

By arrangement with the Editors, the results of the annual Ailsa Craig Gannet census are now being published regularly in the *Scottish Naturalist,* but the results of the previous annual census work appeared in various publications, in particular for some twenty years in the series of *Clyde Seabird Reports* largely created for the Ailsa Gannet census by the Renfrewshire Natural History Society. A useful bibliography of all past census work was given in Gibson (1983), to which interested readers are referred, and references to the immediate past years are given below.

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SCOTTISH WETLAND SPIDERS
1 - PEAT BOGS IN STRATHCLYDE

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Introduction

In spite of the popular view of the Scottish climate and countryside, undisturbed wetland habitats such as marshes and peat bogs are not as ubiquitous as one might imagine. These habitats are under threat from a variety of human activities, with a general trend towards 'reclamation' or development of such 'unproductive' areas, at the expense of complete, irreversible destruction of their natural communities. The net result is that such habitats are now mostly patchy remnants of formerly more extensive wetland areas. As a consequence, their fauna and flora have a certain conservation value; indeed, as far as spiders are concerned, many of the rare species on the British list are inhabitants of wetlands.

The invertebrate species of wetlands are also of interest because of their adaptation to the rather special environmental conditions. In 1977, work commenced on a study of the spiders (Araneida) and harvestmen (Phalangida or Opiliones) at a number of wetland sites in south-west Scotland. Data obtained during the course of this work form the basis for this and subsequent papers. The locations of the sites sampled so far are shown in Figure 1.

Strathclyde Peat Bogs

The peat bogs of Strathclyde are just scattered remnants, often disturbed by man's activities in the form of drainage, afforestation, etc. Twelve sites are considered in this paper.

Some of these sites form pairs which illustrate the effect of disturbance and alteration of habitat from open mire:

I. Carnwath Moss and Carnwath Wood contrast open, wet mire at the former with drier conditions at the latter and birch scrub developing.

II. Braehead Moss and Braehead Wood, with quite dense birch woodland at the latter.

III. Bloak Moss and Bloak Wood, where a dense stand of Scots pine has been planted.

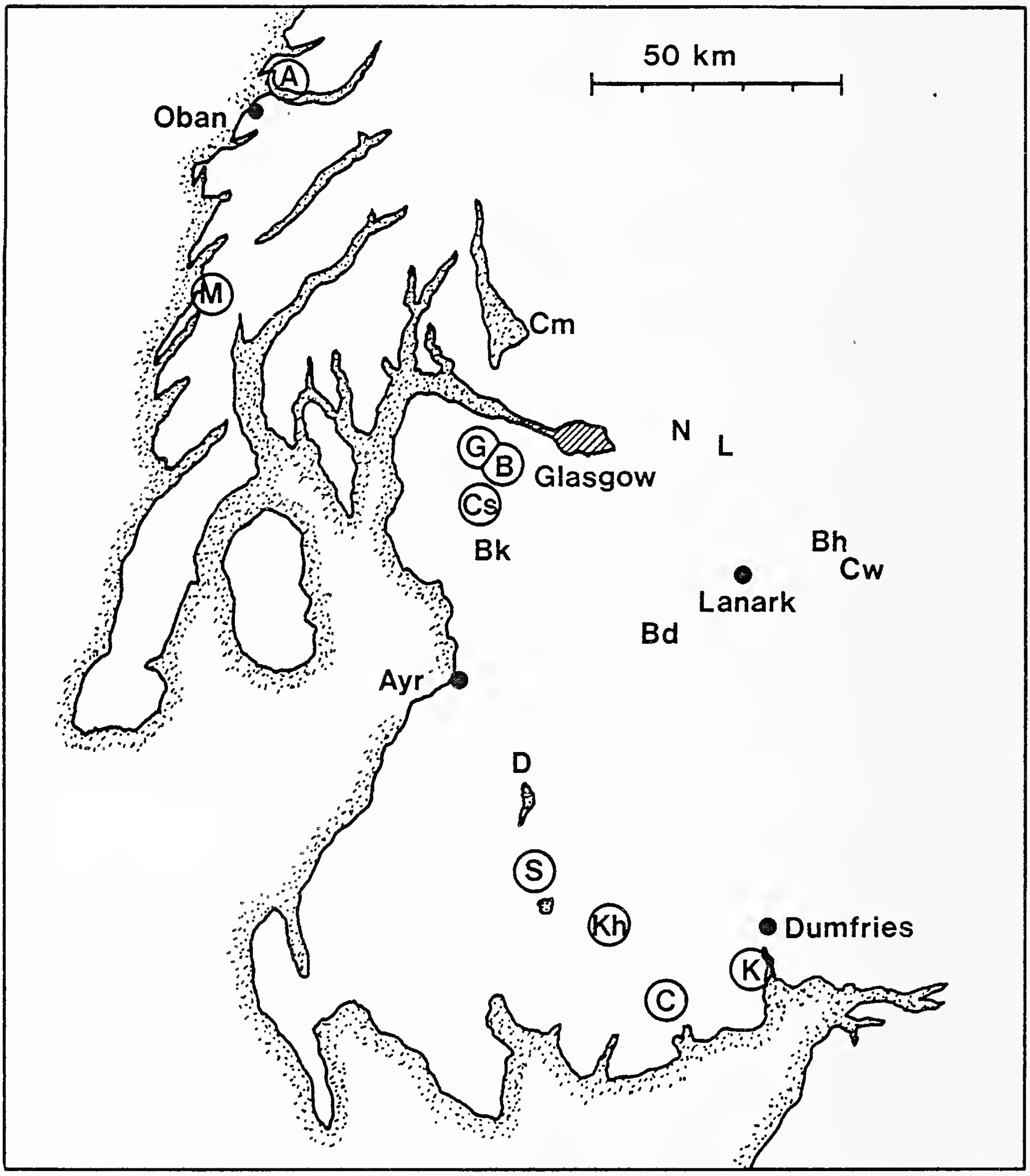

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Figure 1

Map of south-west Scotland showing peatland sites sampled for spiders

Those sampled in 1977 and reported in this paper are as undernoted

Cw - Carnwath Moss (and Wood)
Bh - Braehead Moss (and Wood)
Bk - Bloak Moss (and Wood)
L - Longriggend Moss
N - North Bellstane Plantation (Moor and Wood)
Bd - Blood Moss
D - Dalmellington Moss and Sillyhole Moss

Another location sampled in 1977 was

Cm - Crom Mhin at Loch Lomondside

Also indicated (and encircled) are the undernoted sites sampled in 1978

Argyll:
A - Moss of Achnacree
M - Moine Mhor

Renfrewshire:
G - Glen Moss
B - Barrmufflock Dam
Cs - Castle Semple Loch

Kirkcudbrightshire:
S - Silver Flowe
Kh - Kenmure Holms
C - Carlingwark Loch
K - Kirkconnell Flow

These other wetland communities will be considered in future papers in this series

IV. North Bellstane Plantation has a relatively dry, disturbed open patch of 'moor' flanked by wet birch woodland.

V. At Dalmellington, the short vegetation of Dalmellington Moss contrasts with the taller, fen-like community of the contiguous Sillyhole Moss, probably enriched from the adjacent water course.

The two remaining sites are higher altitude bogs, at Longriggend Moss and Blood Moss.

The aim of the survey carried out in 1977 was to obtain data on the spiders and harvest-spiders at wet terrestrial sites at altitudes below 1000 feet (c. 310m) in order to assess the status of the communities from a conservation point of view.

The vegetation at the sampling stations may be summarised as follows:

1. Carnwath Moss, Lanarkshire: NS975479, altitude 220m. Wet peat bog in exposed position with vegetation dominated by *Erica tetralix*, *Calluna vulgaris*, *Eriophorum angustifolium*, *E. vaginatum*, and *Nardus stricta*, with bryophytes including *Sphagnum magellanicum*, *S. tenellum*, *Polytrichum alpestre*, *Gymnocolea inflata* and *Lepidozea reptans*.

2. Carnwath Wood, Lanarkshire: NS972479, altitude 220m. Drier part of Carnwath Moss with clearer drainage and slightly sheltered by growing *Pinus sylvestris* and *Betula pubescens;* ground vegetation dominated by rather tall, straggly *C. vulgaris* with *N. stricta*, *Pleurozium schreberi*, *Hypnum cupressiforme* var. *ericetorum*, *Polytrichum commune*, *G. inflata*, *L. reptans*, *Aulocomnium palustre*, *Sphagnum papillosum*, *S. cuspidatum*, and *S. fimbriatum*.

3. Braehead Moss, Lanarkshire: NS959508, altitude 280m. Active peat bog in exposed position; fairly tall *C. vulgaris* with a few scattered small *P. sylvestris* trees, and ground vegetation including *N. stricta*, *E. tetralix*, *Sphagnum magellanicum*, *S. papillosum*, *S. tenellum*, *Breutelia chrysosoma*, *P. schreberi*, *H. cupressiforme* var. *ericetorum*, *G. inflata*, *Odontoschisma sphagni* and *Rhytidiadelphus loreus*.

4. Braehead Wood, Lanarkshire: NS959507, altitude 280m. In wet birch wood offering shelter; ground vegetation with sparse short grasses and areas of taller grass or moss clumps, but main feature is the moderate amount of compacted leaf litter.

5. Bloak Moss, Ayrshire: NS368459, altitude 80m. Actively

growing bog in a fairly exposed position, sheltered by plantation to west; dominated by tall *C. vulgaris* with scattered *P. sylvestris* seedlings, *N. stricta*, *S. magellanicum*, *O. sphagni*, *P. schreberi*, *H. cupressiforme* var. *ericetorum*, *Leucobryum glaucum*, and *Cladonia* spp.; dissected by drainage ditches which are largely blocked.

6. Bloak Wood, Ayrshire: NS368459, altitude 80m. *P. sylvestris* plantation at Bloak Moss giving sheltered conditions for the ground layer, which is a poorer representation of the vegetation community of the open moss; dominated by tall *C. vulgaris*, much less active *Sphagnum* spp. in drier and better drained situation, and areas of bare peat surface with pine needle cover.

7. Longriggend Moss, Lanarkshire: NS814697, altitude 220m. Very exposed peat bog, with rather short *C. vulgaris*, *E. tetralix*, *E. vaginatum*, *N. stricta*, *P. commune*, and *Vaccinium myrtillus;* actively growing *Sphagnum papillosum*, *S. magellanicum* and *Vaccinium oxycoccus* in congested drainage ditch.

8. North Bellstane Plantation (NBP) 'Moor', Lanarkshire: NS755717, altitude 110m. Fairly sheltered heath, much disturbed by forestry operations, with shallow peat over rocks; tall *C. vulgaris*, *D. flexuosa*, scattered small specimens of *P. sylvestris* and *Betula pubescens*, patches of *Sphagnum* spp. and *Polytrichum* spp.

9. North Bellstane Plantation (NBP) Wood, Lanarkshire: NS755718, altitude 110m. *B. pubescens* woodland offering shelter to wet ground layer in which the vegetation includes *V. myrtillus*, *E. tetralix*, *C. vulgaris*, *D. flexuosa*, *Juncus acutiflorus*, *Sphagnum palustre*, *S. cuspidatum*, *Lophocolea bidentata*, *Hypnum cupressiforme* and *Plagiothecium undulatum.*

10. Blood Moss, Lanarkshire: NS682326, altitude 300m. Fairly exposed active peat bog with very short vegetation including *C. vulgaris*, *E. tetralix*, *E. vaginatum*, *E. angustifolium*, *N. stricta*, *H. cupressiforme* var. *ericetorum*, *V. oxycoccus*, *Cladonia* spp., *Sphagnum capillacium*, *S. tenellum*, *S. cuspidatum*, *S. fuscum*, *S. imbricatum*, *S. magellanicum* and *S. papillosum.*

11. Dalmellington Moss, Ayrshire: NS466064, altitude 170m. An exposed peat bog with a fairly short vegetation, which includes *C. vulgaris*, *E. tetralix*, *Molinia caerulea*, *Trichophorum cespitosum*, *E. vaginatum*, *E. angustifolium*, *Sphagnum* spp. and *Polytrichum* spp., interspersed with *Myrica gale.*

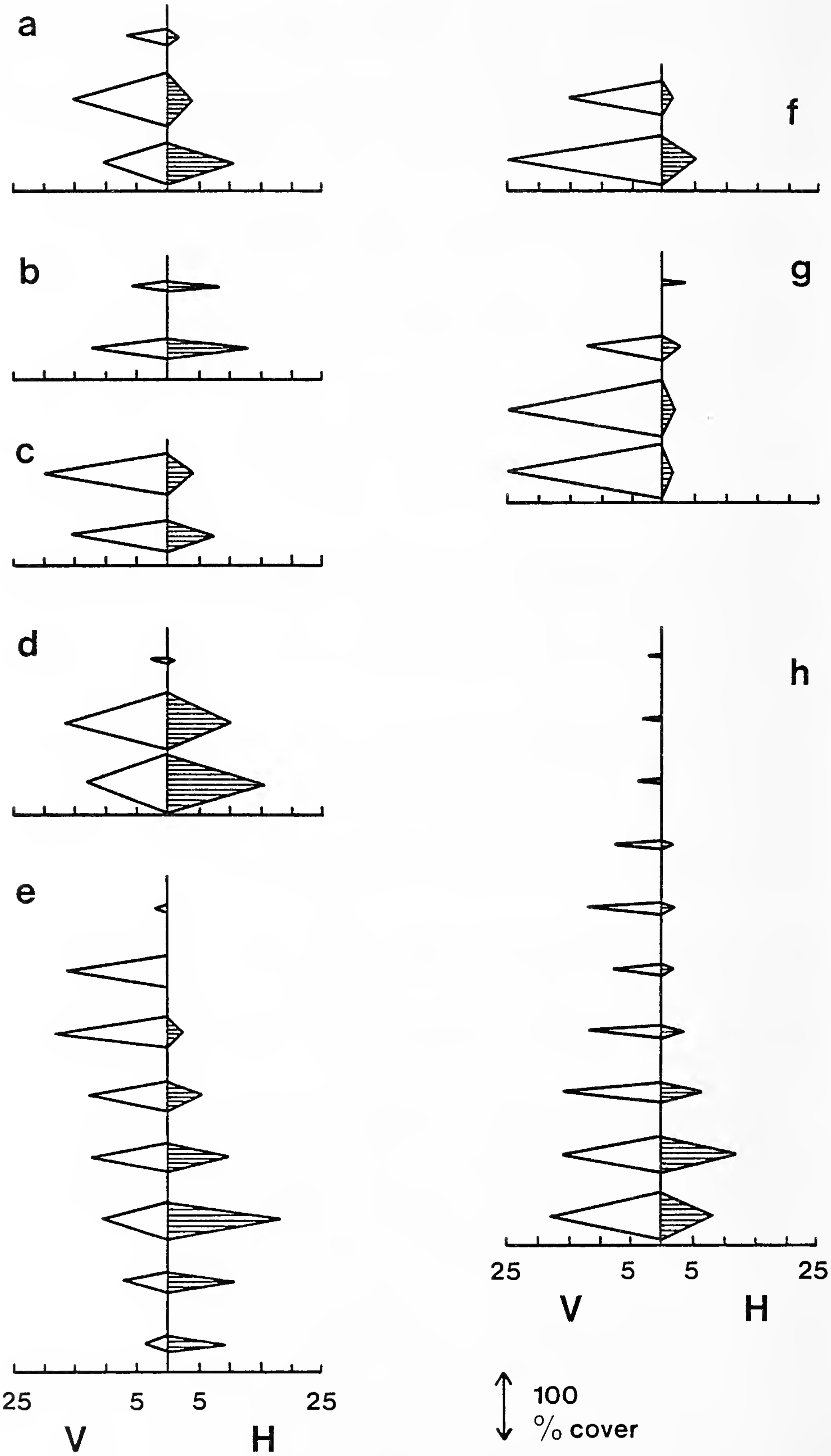
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Figure 2

Vegetation profiles

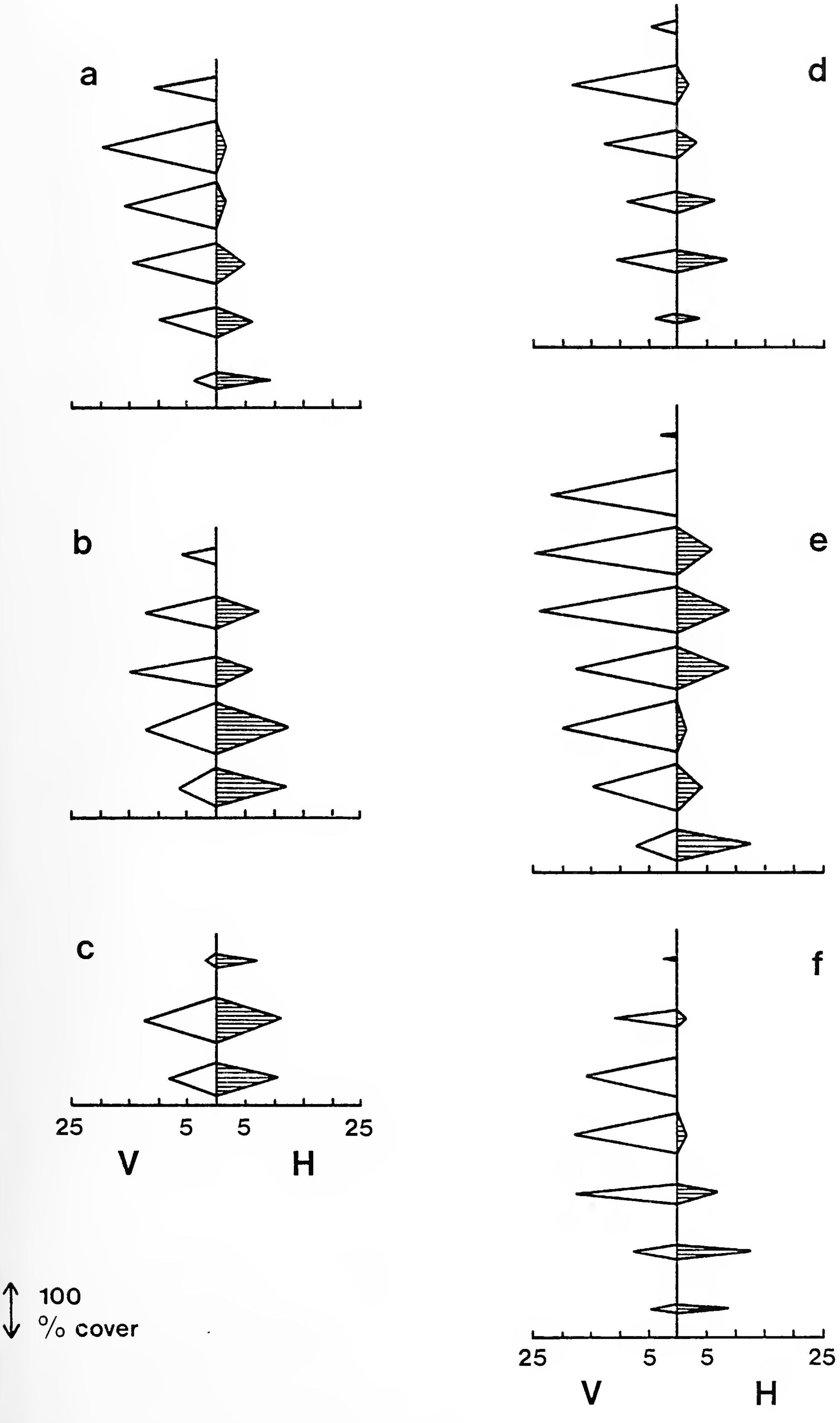
(a) Longriggend Moss; short *Calluna vulgaris*.
(b) Blood Moss; sparse *Eriophorum vaginatum*.
(c) Blood Moss; short *C. vulgaris*.
(d) Carnwath Moss; very dense short *C. vulgaris* and *Erica tetralix*.
(e) Carnwath Wood; tall, mature or degenerating *C. vulgaris*.
(f) Dalmellington Moss; young *C. vulgaris*, short and dense.
(g) Dalmellington Moss; *E. vaginatum* tussock.
(h) Sillyhole Moss; tall but sparse grassy vegetation.

For each trapezoid, which represents vegetation at a successive 10 cm height, the vertical axis is proportional to the density of vegetation; the left-hand apex is placed according to the frequency of vertical structures and the right-hand (shaded part) reflects the frequency of horizontal features.

Figure 3

Vegetation profiles

(a) North Bellstane Plantation Moor; with mature *Calluna vulgaris*.
(b) North Bellstane Plantation Wood; with shrubby *C. vularis* and *Vaccinium myrtillus*.
(c) North Bellstane Plantation Wood; with *Deschampsia flexuosa* clump.
(d) Braehead Moss; mature *C. vulgaris*.
(e) Bloak Moss; mature *C. vulgaris*.
(f) Bloak Wood; degenerating *C. vulgaris*.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100
% cover

12. (Dalmellington) Sillyhole Moss, Ayrshire: NS465063, altitude 170m. Willow carr at edge of Dalmellington Moss near Parrie Burn; vegetation (tall in spring/summer) with *Carex rostrata*, *Angelica sylvestris*, *Epilobium palustre*, some *Scirpus sylvaticus* and a fairly deep underlying moss layer.

These vegetation descriptions relate to the areas immediately surrounding the pitfall sampling stations, and are by no means complete lists for the sites. They exclude, for example, the large amounts of *V. oxycoccus* present in wet hollows at Carnwath Moss, and interesting records such as *Andromeda polifolia* at Bloak and Dalmellington Mosses. The vegetation of peatland sites is the subject of separate survey work by Dr. E.M. Bignal of the Nature Conservancy Council.

Longriggend and Dalmellington Mosses were burned during the course of the sampling.

The plant species composition at most of the sites is very similar but varies greatly in physiognomy. A vertical quadrat method (Curtis and Bignal 1978, Curtis 1980) was used to describe the structure of the vegetation at random points close to the pitfall sample stations. A vertical series of 10 x 10 cm quadrats, subdivided into twenty-five 2 x 2 cm squares, was described in terms of frequency of vegetation structures with inclination greater than 45° ('vertical'), frequency of structures with inclination less than 45° ('horizontal') and percentage cover density of vegetation, viewed horizontally through the quadrat; the structures within a 10 cm cube at successive heights were thus described.

These vegetation structure parameters are illustrated in Figures 2 and 3, excluding site 4 (Braehead Wood) where the vegetation at the sampling station is only short, sparse grass with moderate amounts of dead birch leaves and bare earth. The most obvious distinction is the separation of the heather-dominated sites into two groups: those with low plants - Blood, Carnwath, Dalmellington and Longriggend Mosses, although the heather at the last site is a little taller - and the others with taller shrubs. The latter may be fairly dense at all levels - Bloak Moss and Carnwath Wood (where the heather is less dense) or rather bushier with an increasing frequency of shoots in the upper layers - NBP 'Moor', Bloak Wood and Braehead Moss. The heather in NBP Wood comprises rather isolated clumps, dense at the base and tapering away gradually in terms of both vertical and horizontal structures. Sillyhole Moss shows great height (as recorded in early spring) but rapid reduction in vegetation density with height; this structure varies greatly with the seasons, in contrast to the relatively permanent heather structures.

These physiognomic variations in the vegetation will effect the spiders and phalangids at the sites, by determining the availability of distinct physical locations for the animals' activities such as hunting and web-building. They will also affect the microclimatic conditions and this will result in varying araneid/phalangid communities, as will the amount of litter on the soil or peat surface, since this varies with the height of the overlying vegetation. These variations are additional to any effects resulting from surrounding bushes and trees, and will combine with the influence of altitude, exposure, etc. The relationship between the araneid/phalangid community and spatial variations in vegetation physiognomy will be considered in a separate paper.

Sampling Method

Pitfall traps were the main technique used, since they operate continuously over the sampling period to capture any species active on the ground surface. In the sites of this study, without much vegetation higher than the ground or lower field layers, this technique should provide very good coverage of the spider and phalangid species present. Small quantities of trapping/killing/preserving fluid (3.5% formalin with some detergent) were used in the traps. Ten traps were set within approximately one square metre at each site and emptied at about monthly intervals. The trapping period considered here covered spring and summer of 1977.

Specimens were preserved in 70% ethanol. Araneida and Phalangida were determined, and nomenclature followed is that of Locket and Millidge (1951,1953) and Locket, Millidge and Merrett (1974) for spiders, and Sankey and Savory (1974) for harvestmen. Other arthropods have been retained, and are available for study.

Species Recorded

A list of the species included in the 5,876 specimens collected and considered here is given in Appendix 1; these included 126 species of spiders and seven species of phalangids, as well as several immatures. The number of species recorded (i.e. species richness) in relation to the general characteristics of the sites is expressed in Table 1.

In terms of representation of different families, listed in Appendix 2, all sites show similar features, with a predominance of Linyphiidae typical of northern localities. This dominance by linyphiids is moderated only by the numbers of wolf-spiders (Lycosidae) also found in these habitats.

Table 1

Species Richness

The number of species recorded in relation to the general characteristics of the sites

		Short vegetation		Tall vegetation	
	Altitude (m)	Open terrain	Woodland	Open terrain	Woodland
Bloak	80	--	--	29	34
NBP	110	--	--	47	52
Dalmellington	170	31	--	46	--
Carnwath	220	47	--	--	49
Longriggend	220	46	--	--	--
Braehead	280	--	39	37	--
Blood	300	22	--	--	--

Average values of species richness for different categories of sites may be compared as follows:

(a) Vegetation physiognomy - short (5 sites) 37
- tall (7 sites) 42

(b) Site exposure - open terrain (8 sites) 38
- woodland (4 sites) 44

(c) Altitude - below 200m (6 sites) 40
- above 200m (6 sites) 40

These values suggest that the effects of site physiognomy and exposure/habitat type are more influential than altitude.

While some of the species recorded are to be found in a variety of habitats, many are characteristic of wet places. The more numerous species captured tended to prefer one type of habitat relative to another and are considered here.

Species found only at wetter sites were *Pardosa amentata*, *Oedothorax fuscus*, and *O. retusus*. Species more abundant at wet rather than dry sites were *Pardosa pullata*, *Trochosa terricola* (except at Bloak), *Pirata piraticus*, *Antistea elegans*, *Araeoncus crassiceps* (especially at Longriggend) and *Silometopus elegans*.

Species taken more at open moss sites than in woods were *Pardosa nigriceps*, *Alopecosa pulverulenta*, *Walckenaera antica* (except at Carnwath), *Cnephalocotes obscurus* and *Centromerita concinna*. In contrast, *Monocephalus fuscipes*, *Agyneta cauta*, *Microneta viaria* and *Macrargus rufus* occurred more in woods (Carnwath, Braehead and NBP) and *Tapinocyba pallens* was recorded maximally at sites with tall heather (Carnwath Wood, Braehead Moss, North Bellstane Plantation).

The following species were very restricted in the sites at which they were captured: *Maso sundevalli* (Carnwath Wood), *Diplocentria bidentata* (Braehead Moss), *Agyneta subtilis* (Bloak Wood), *Trichopterna mengei* (Longriggend Moss), *Centromerita bicolor* (Dalmellington Moss), *Lophomma punctatum* (Sillyhole Moss), *Pocadicnemis pumila* (mostly at NBP Wood), *Lepthyphantes tenebricola* (Blood Moss and Carnwath Wood) and *Lepthyphantes mengei* (Longriggend Moss, NBP).

Rare Species

The distribution of the following species is discussed relative to the distribution maps of Locket, Millidge and Merrett (1974).

(a) Species recorded for the first time in Scotland.

Baryphyma pratensis at Braehead Moss, and also recorded at Crom Mhin, Loch Lomond, during this survey; a rare species found in English counties in grass and herbage in damp meadows, usually near streams, rivers etc.

Hahnia pusilla at Dalmellington Moss; an uncommon species, but fairly widespread in England and Wales, often in damp situations.

(b) Species extremely rare in Scotland.

Hilaira pervicax, taken at Sillyhole Moss, had previously been recorded at very few localities, in wet moss: Whitfield Fell (Northumberland at altitude 470m), Red Tarn, Helvellyn, Pennines and Lake District, Migneint in Caernarvonshire. The only other Scottish sites are Loch Craggie (Sutherland), Inverpolly (Ross and Cromarty) and near Aviemore.

(c) Rare species which are localised in occurrence.

Euryopis flavomaculata (Carnwath and Bloak Woods, Dalmellington Moss), *Hypselistes jacksoni* (Carnwath Moss and Wood, Longriggend Moss and Sillyhole Moss), *Gongylidiellum latebricola* (Braehead Moss and Wood, Bloak Wood) and *Linyphia* (*Neriene*) *marginata* (NBP 'Moor'), a Scottish species known from only a few localities.

(d) Rare but widespread species.

Drassodes pubescens (Carnwath Wood), *Robertus arundineti* and *Walckenaera melanocephala* (Carnwath Moss), *Walckenaera vigilax* (Bloak Moss and Wood), *Silometopus elegans* (Carnwath, Longriggend, Blood and Sillyhole Mosses), *Araeoncus crassiceps* (Carnwath, Longriggend, Blood, Dalmellington and Sillyhole Mosses), *Meioneta beata* (Longriggend Moss) and *Maro minutus* (Carnwath, Bloak and NBP woods).

Conclusion

The purpose of the survey producing these data was to provide basic information which could be used in assessing the conservation value of the communities. An ordination method has been devised to facilitate this (Curtis 1979 and in prep.), but general aspects may be considered here. It is clear that the sites surveyed are all worthy of conservation from an arachnological point of view. The 'better' sites support the valuable species indicated above, and even the other sites are uniquely known locations within their county for many species.

In spite of its interesting features, NBP 'Moor' could be considered as an example of the effects of disturbance on this type of habitat. It appears that certain rare species have been eliminated, and replaced by more common species which can tolerate the different conditions present at different stages of the disturbance, whether denudation or afforestation. Thus there results a mixture of common species typical of heathland with other common species from woodland.

In contrast, the disturbance at Bloak Moss by afforestation has produced a more interesting spider community at the Bloak Wood sampling station. This is contingent on the persistence of the wetland ground vegetation and moist conditions; it will not be the case deeper in the wood, or in denser plantations where the ground flora is eliminated or drainage more efficient.

The sites of particular interest are, on the whole, the wetter sites - Carnwath, Sillyhole, Dalmellington and Longriggend Mosses; as a corollary, the most interesting species are characteristic of wetlands. Clearly the greatest danger to these is alteration of the water level (apart from complete obliteration of the habitat). A rise in the water table, with subsequent flooding, would have drastic consequences but might still possibly manifest an interesting fauna. More seriously, improvements in or implementation of drainage would effectively eliminate the moisture-dependent wetland species and destroy these spider communities.

While these wetland sites may appear to be of little use to the general human populace in terms of scenic value, recreational assets, building or agricultural use, they do retain communities - including the spiders described in this paper - which are an essential component of the ecosystem from which we cannot divorce ourselves. Disruption of these ecological conditions is not simply a matter of short-term exploitation in terms of the kind of 'profit' human agencies can make from them, but must be considered more in terms of the maintenance of a viable environment for ourselves and the ecosystem in which we must survive.

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Appendix 1

Spiders (Araneida) and harvestmen (Phalangida) recorded at twelve peatland sites in Strathclyde, spring and summer 1977.

Note the high proportion of new county records, indicated by the letters A and L for Ayrshire and Lanarkshire respectively.

	Site number												
	1	2	3	4	5	6	7	8	9	10	11	12	
ARANEIDA													
Amaurobiidae													
Amaurobius similis (Blackwall)	-	-	-	-	-	-	-	-	-	-	+	-	
Dictynidae													
Dictyna arundinacea (L.)	+	-	+	-	-	-	-	+	-	-	-	-	
Gnaphosidae													
Drassodes lapidosus (Walckenaer)	-	-	-	+	+	+	+	+	-	-	-	-	AL
D. pubescens (Thorell)	-	+	-	-	-	-	-	-	-	-	-	-	L
Haplodrassus signifer (C.L. Koch)	-	-	-	+	+	+	+	-	-	+	+	+	L
Micaria pulicaria (Sundevall)	-	+	-	-	-	-	+	+	-	-	-	-	
Clubionidae													
Clubiona reclusa O.P.-Cambridge	-	+	-	+	-	-	-	-	-	-	-	+	
C. lutescens Westring	-	-	-	-	-	-	-	-	+	-	-	-	
C. trivialis C.L.K.	+	+	+	-	+	+	+	+	+	-	+	-	A
C. diversa O.P.-C.	-	-	-	-	-	-	-	+	-	-	-	-	
Agroeca proxima (O.P.-C.)	+	-	-	-	-	-	-	+	-	-	-	-	L
Phrurolithus festivus (C.L.K.)	-	-	-	-	-	-	-	-	-	-	+	-	A
Thomisidae													
Xysticus cristatus (Clerck)	+	-	+	-	+	-	+	+	+	+	+	+	
Oxyptila trux (Blackwall)	+	-	+	-	+	+	-	-	-	+	-	+	
Tibellus maritimus (Menge)	+	-	-	-	-	-	-	-	-	-	+	+	AL
Salticidae													
Salticus scenicus (Clerck)	-	-	-	-	-	-	-	-	-	-	-	+	
Lycosidae													
Pardosa palustris (L.)	-	-	-	-	-	-	+	-	-	-	+	-	
P. pullata (Clerck)	+	+	+	-	+	+	+	+	+	+	+	+	
P. prativaga (L. Koch)	-	-	+	+	-	-	-	-	-	-	-	-	L
P. amentata (Clerck)	-	-	-	-	-	-	+	-	+	-	-	+	
P. nigriceps (Thorell)	+	+	+	+	+	+	-	+	+	+	+	+	
Alopecosa pulverulenta (Clerck)	+	+	+	+	+	+	+	+	+	+	+	+	

	Site number												
	1	2	3	4	5	6	7	8	9	10	11	12	
Trochosa terricola Thorell	+	+	+	+	+	+	+	+	+	+	+	+	
Pirata piraticus (Clerck)	+	+	+	+	+	−	+	+	+	+	+	+	
P. piscatorius (Clerck)	−	−	−	−	−	+	−	−	−	−	−	−	A
P. uliginosus (Thorell)	+	−	−	−	+	+	−	−	−	−	+	+	AL
Agelenidae													
Cryphoeca silvicola (C.L.K.)	−	+	−	+	−	+	−	+	−	−	−	−	
Antistea elegans (Blackwall)	+	−	−	−	+	−	+	+	+	+	+	+	A
Hahnia pusilla C.L.K.	−	−	−	−	−	−	−	−	−	−	+	−	A
Mimetidae													
Ero cambridgei Kulczynski	+	−	−	−	−	−	−	−	−	−	−	−	
E. furcata (Villers)	−	−	−	−	−	+	−	−	+	−	−	−	
Theridiidae													
Euryopis flavomaculata (C.L.K.)	−	+	−	−	−	+	−	−	−	−	+	−	AL
Theridion bimaculatum (L.)	−	−	−	−	−	−	−	+	+	−	−	−	
Robertus lividus (Blackwall)	+	+	+	+	−	−	+	+	+	−	+	+	
R. arundineti (O.P.-C.)	+	−	−	−	−	−	−	−	−	−	−	−	L
Tetragnathidae													
Pachygnatha clercki Sundevall	+	−	−	−	−	−	+	+	+	−	+	+	
P. listeri Sundevall	−	−	−	−	−	−	−	−	+	−	−	+	
P. degeeri Sundevall	−	−	+	+	−	−	+	+	+	−	+	+	
Meta mengei (Blackwall)	−	−	−	+	+	−	−	−	+	−	−	−	
Araneidae													
Araneus quadratus Clerck	−	−	−	−	+	−	−	−	−	−	−	−	
Linyphiidae													
Ceratinella brevipes (Westring)	+	+	+	+	+	+	+	+	+	−	−	+	
C. brevis (Wider)	+	−	+	−	−	−	−	+	−	−	+	+	
Walckenaera acuminata Blackwall	−	+	−	+	−	−	+	+	+	−	−	+	
W. antica (Wider)	+	+	+	+	+	+	+	+	+	+	+	−	L
W. melanocephala O.P.-C.	+	−	−	−	−	−	−	−	−	−	−	−	L
W. nudipalpis (Westring)	+	+	+	+	+	+	+	+	+	+	+	+	AL
W. cuspidata Blackwall	+	+	−	+	−	−	−	+	+	−	−	+	
W. vigilax (Blackwall)	−	−	−	−	+	+	−	−	−	−	−	−	
Dicymbium brevisetosum Locket	−	−	−	−	−	−	+	−	−	−	−	−	L
Gnathonarium dentatum (Wider)	−	−	−	−	−	−	+	−	−	−	−	−	
Dismodicus bifrons (Blackwall)	−	−	−	−	−	+	−	−	+	−	−	−	
Hypomma bituberculatum (Wider)	−	−	−	−	+	−	−	−	−	−	−	+	
Metopobactrus prominulus (O.P.-C.)	−	−	−	−	−	−	+	−	−	−	−	−	L
Baryphyma pratensis (Blackwall)	−	−	+	−	−	−	−	−	−	−	−	−	L

	Site number												
	1	2	3	4	5	6	7	8	9	10	11	12	
Gonatium rubens (Blackwall)	+	+	+	-	+	-	+	+	+	-	-	+	
Maso sundevalli (Westring)	-	+	-	+	-	-	-	+	+	-	-	-	
Peponocranium ludicrum (O.P.-C.)	+	-	+	-	+	+	-	-	-	-	+	-	
Pocadicnemis pumila (Blackwall)	-	-	+	+	+	+	-	+	+	-	-	+	
Hypselistes jacksoni (O.P.-C.)	+	+	-	-	-	-	+	-	-	-	-	+	AL
Oedothorax tuberosus (Blackwall)	-	-	-	-	-	-	-	-	+	-	-	-	L
O. retusus (Westring)	-	-	-	-	-	-	-	-	+	-	-	-	
Trichopterna thorelli (Westring)	-	-	-	-	-	-	-	-	-	-	+	-	A
T. mengei (Simon)	-	+	+	+	-	-	+	+	+	-	-	+	L
Silometopus elegans (O.P.-C.)	+	-	-	-	-	-	+	-	-	+	-	+	L
Cnephalocotes obscurus (Blackwall)	-	-	+	+	+	+	+	+	+	-	+	-	
Minyriolus pusillus (Wider)	-	+	+	-	-	-	-	-	-	-	-	-	
Tapinocyba pallens (O.P.-C.)	-	+	+	+	+	-	+	+	+	-	-	-	
Monocephalus fuscipes (Blackwall)	-	+	-	+	-	-	-	+	+	-	+	+	
Lophomma punctatum (Blackwall)	-	-	-	-	-	-	+	-	-	-	-	+	
Gongylidiellum vivum (O.P.-C.)	+	-	-	-	-	-	-	-	-	-	-	-	
G. latebricola (O.P.-C.)	-	-	+	+	-	+	-	-	-	-	-	-	AL
Micrargus herbigradus (Blackwall)	+	+	+	+	-	+	+	+	+	-	-	+	A
Erigonella hiemalis (Blackwall)	-	-	-	+	-	-	-	-	+	-	-	-	L
Savignya frontata (Blackwall)	-	+	+	+	-	-	+	-	-	-	+	-	
Diplocephalus permixtus (O.P.-C.)	+	-	-	-	-	-	-	-	-	-	-	+	
D. picinus (Blackwall)	-	+	-	+	-	-	-	-	+	-	-	-	
Araeoncus crassiceps (Westring)	+	-	-	-	-	-	+	-	-	+	+	+	AL
Diplocentria bidentata (Emerton)	-	-	+	-	-	-	-	-	-	-	-	-	L
Erigone dentipalpis (Wider)	-	-	-	-	-	-	-	+	-	-	-	-	
E. atra (Blackwall)	-	+	-	-	-	-	+	-	-	+	-	-	
Drepanotylus uncatus (O.P.-C.)	-	-	-	-	-	-	-	-	-	-	-	+	A
Hilaira pervicax Hull	-	-	-	-	-	-	-	-	-	-	-	+	A
Aphileta misera (O.P.-C.)	-	-	-	-	+	-	-	-	-	-	-	-	A
Porrhomma pygmaeum (Blackwall)	-	+	-	+	-	-	-	-	-	-	-	-	
P. pallidum Jackson	-	+	-	-	-	-	-	-	-	+	-	-	
Agyneta subtilis (O.P.-C.)	-	-	-	-	-	+	-	-	-	-	-	+	A
A. conigera (O.P.-C.)	-	-	-	+	-	-	-	-	+	-	-	-	L
A. decora (O.P.-C.)	+	+	-	-	-	-	+	-	-	-	-	-	L
A. cauta (O.P.-C.)	-	+	+	+	+	-	+	-	-	+	-	-	AL
Meioneta saxatilis (Blackwall)	+	-	-	-	-	-	+	-	-	-	-	-	L
M. beata (O.P.-C.)	-	-	-	-	-	-	+	-	-	-	-	-	L
Microneta viaria (Blackwall)	-	+	-	+	-	+	-	+	+	-	-	-	
Maro minutus O.P.-C.	-	+	-	-	-	+	-	-	+	-	-	-	L
Centromerus sylvaticus (Blackwall)	-	+	-	+	-	-	-	-	-	-	-	-	
C. expertus (O.P.-C.)	+	-	-	-	-	-	-	-	-	-	-	+	AL
C. prudens (O.P.-C.)	+	-	-	-	-	-	-	-	-	-	-	-	
C. arcanus (O.P.-C.)	-	-	-	-	-	-	-	-	-	+	-	-	L
C. dilutus (O.P.-C.)	-	+	-	-	-	-	-	+	+	-	-	-	

	Site number												
	1	2	3	4	5	6	7	8	9	10	11	12	
Centromerita bicolor (Blackwall)	-	-	-	-	-	-	-	+	-	-	+	-	
C. concinna (Thorell)	+	-	+	-	+	-	+	-	-	+	+	+	
Oreonetides abnormis (Blackwall)	+	+	+	+	-	+	-	+	+	+	-	-	A
Macrargus rufus (Wider)	-	+	-	+	-	-	-	-	+	-	-	-	
Bathyphantes approximatus (O.P.-C.)	-	-	-	-	-	-	-	-	-	-	-	+	
B. gracilis (Blackwall)	+	-	-	-	-	-	+	+	+	-	-	+	
B. parvulus (Westring)	+	-	-	-	-	-	-	+	-	-	-	+	L
B. nigrinus (Westring)	-	-	-	-	-	-	-	-	+	-	-	+	
Kaestneria dorsalis (Wider)	-	-	-	-	-	-	+	-	-	-	-	-	
K. pullata (O.P.-C.)	-	-	-	-	-	-	-	-	-	-	-	+	
Diplostyla concolor (Wider)	-	-	-	-	-	+	-	-	+	-	-	-	
Poeciloneta globosa (Wider)	+	-	-	-	-	-	-	-	-	-	-	-	
Stemonyphantes lineatus (L.)	+	-	-	-	-	-	+	-	+	-	-	-	
Bolyphantes alticeps (Sundevall)	-	-	-	-	-	-	-	-	-	+	-	-	
Lepthyphantes minutus (Blackwall)	-	-	-	-	-	+	-	-	-	-	-	-	
L. alacris (Blackwall)	-	-	-	-	-	+	-	+	+	-	-	-	
L. whymperi F.O.P.-Cambridge	-	-	-	-	-	-	+	-	-	-	-	-	L
L. obscurus (Blackwall)	-	+	-	-	-	-	-	-	-	-	-	-	
L. zimmermanni Bertkau	+	+	+	+	+	-	-	+	+	-	-	-	
L. cristatus (Menge)	-	-	-	-	-	+	-	-	-	-	-	-	
L. mengei Kulczynski	-	-	-	-	-	-	+	+	+	+	-	-	L
L. tenebricola (Wider)	-	+	+	+	-	-	-	-	+	-	-	-	
L. ericaeus (Blackwall)	-	+	+	-	-	-	+	+	+	-	+	+	A
L. pallidus (O.P.-C.)	+	-	-	-	-	-	-	-	-	-	-	-	
L. pinicola Simon	-	-	+	-	-	-	-	-	-	-	-	-	L
Linyphia (Neriene) montana (Cl.)	-	-	-	-	-	-	-	+	-	-	-	-	
L. (N.) marginata C.L.K.	-	-	-	-	-	+	-	-	-	-	-	-	A
Microlinyphia pusilla (Sundevall)	+	+	-	+	-	-	+	+	+	+	-	+	

PHALANGIDA

Nemastoma bimaculatum (Fabricius)	+	+	+	-	+	+	-	-	-	-	-	-
Mitopus morio (Fabricius)	+	+	+	+	-	-	+	+	-	-	-	-
Oligolophus tridens (C.L.K.)	-	+	-	-	-	-	-	-	-	-	-	-
O. agrestis (Meade)	-	+	-	-	-	-	-	-	-	-	-	-
Lacinius ephippiatus (C.L.K.)	-	+	-	-	-	-	-	-	-	-	-	-
Platybunus triangularis (Herbst)	-	-	-	-	-	-	-	+	+	-	-	-
Megabunus diadema (Fabricius)	+	+	-	-	-	+	-	-	-	-	-	-

Appendix 2

Number of species in different families.

	All sites	Site number											
		1	2	3	4	5	6	7	8	9	10	11	12
ARANEIDA													
Amaurobiidae	1	-	-	-	-	-	-	-	-	-	-	1	-
Dictynidae	1	1	-	-	-	-	-	-	1	-	-	-	-
Gnaphosidae	4	-	2	-	2	2	2	3	2	-	1	1	1
Clubionidae	6	2	2	1	1	1	1	1	3	2	-	2	1
Thomisidae	3	3	-	2	-	2	1	1	1	1	2	2	3
Salticidae	1	-	-	-	-	-	-	-	-	-	-	-	1
Lycosidae	10	6	5	6	5	6	6	6	5	6	5	7	7
Agelenidae	3	1	1	-	1	1	1	1	2	1	1	2	1
Mimetidae	2	1	-	-	-	-	1	-	-	1	-	-	-
Theridiidae	4	2	2	1	1	-	1	1	2	2	-	2	1
Tetragnathidae	4	1	-	1	2	1	-	2	2	4	-	2	3
Araneidae	1	-	-	-	-	1	-	-	-	-	-	-	-
Linyphiidae	86	27	31	23	26	14	19	30	27	34	13	12	28
PHALANGIDA													
Nemastomatidae	1	1	1	1	-	1	1	-	-	-	-	-	-
Oligolophinae	4	1	4	1	1	-	-	1	1	-	-	-	-
Phalangiidae	2	1	1	-	-	-	1	-	1	1	-	-	-
Total	133	47	49	37	39	29	34	46	47	52	22	31	46

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BREEDING BIOLOGY OF THE CHOUGH ON ISLAY, 1981-1982

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Introduction

There is little information regarding the breeding biology of the Chough *Pyrrhocorax pyrrhocorax* in Britain. In the eastern parts of its range the Chough frequents human habitation and breeds in occupied buildings, but in Britain it usually selects inaccessible nest sites on sea cliffs or ledges in caves (Coombs 1978). The nest is a large structure, made of small sticks and woody stems lined thickly with wool, hair, dead grass and other soft material (Goodwin 1976). In many areas of Britain it is made solely of heather and lined with sheep's wool (Holyoak 1972). The 3 to 5 eggs (rarely 2, 6 or 7) are laid in April and May and incubation, undertaken by the female only, lasts 17 to 18 days, with nestlings fledging between 36 and 41 days.

In Scotland, a survey of breeding Choughs was made on Islay in May 1976 (Booth and Taylor, pers. comm.), an earlier survey in 1963 (Rolfe 1966) being incomplete. Since then, two population counts on the island have been carried out, in 1980 and 1981, together with a breeding survey in 1981 (Warnes 1982). In the following year (1982) an international survey of Choughs was organised by the Royal Society for the Protection of Birds, the British Trust for Ornithology, the Irish Wildbird Conservancy, and La Société pour l'Etude et la Protection de la Nature en Bretagne. This was the first complete survey of Choughs in Wales, the Isle of Man, Scotland, Ireland and Brittany (Bullock, Drewett and Mickleburgh 1983 a,b,c, and in press; Warnes 1983), and during this the Islay population and breeding surveys were repeated. The results of these breeding surveys on Islay in 1981 and 1982 are presented here and discussed in the light of the intervening severe winter. Information on nest site selection, nestling feeding, and details of a Chough ringing programme on Islay, are also presented.

Nest Site Selection

Choughs on Islay nest mainly on sea cliffs, but some pairs nest on inland cliffs and in buildings (Table 1). On the Oa (see Figure 2) all nests were on the coast, but on the Rhinns a sizeable proportion of the nests were on inland cliffs and in

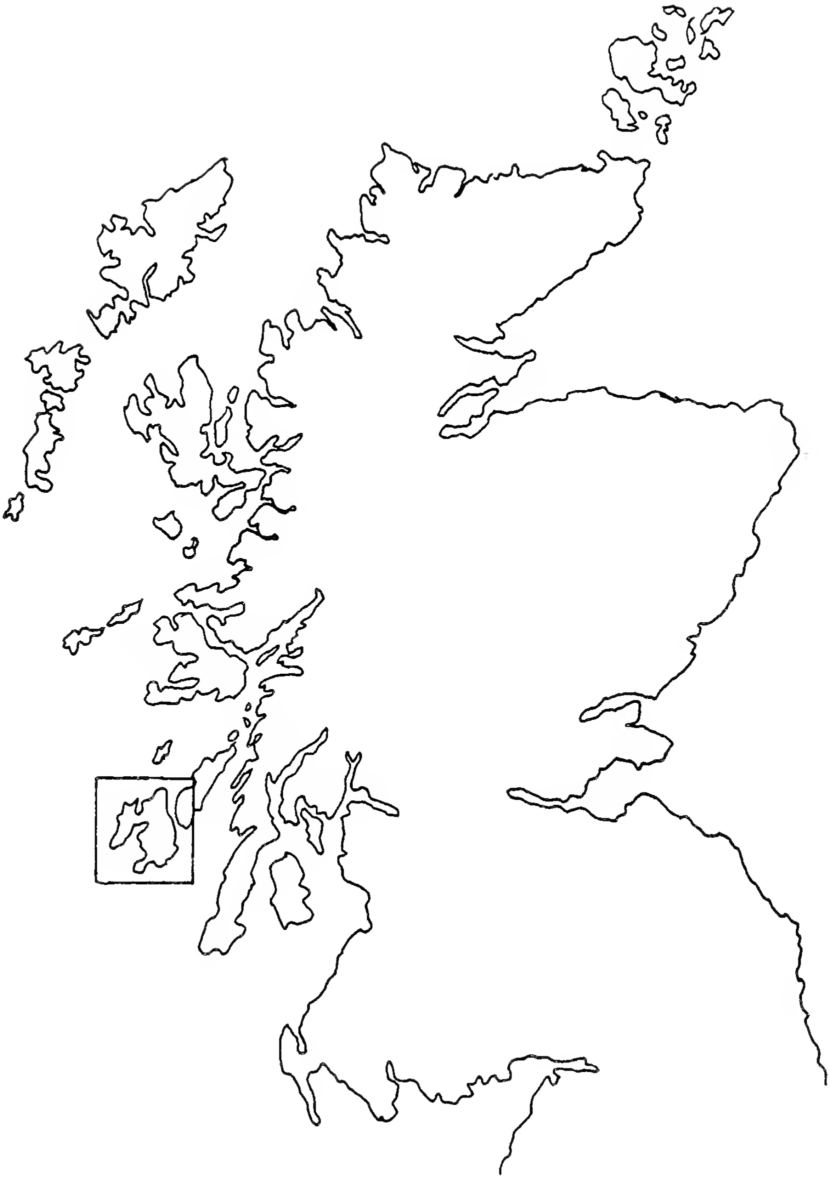

Figure 1

Map of Scotland, showing the location of the Isle of Islay

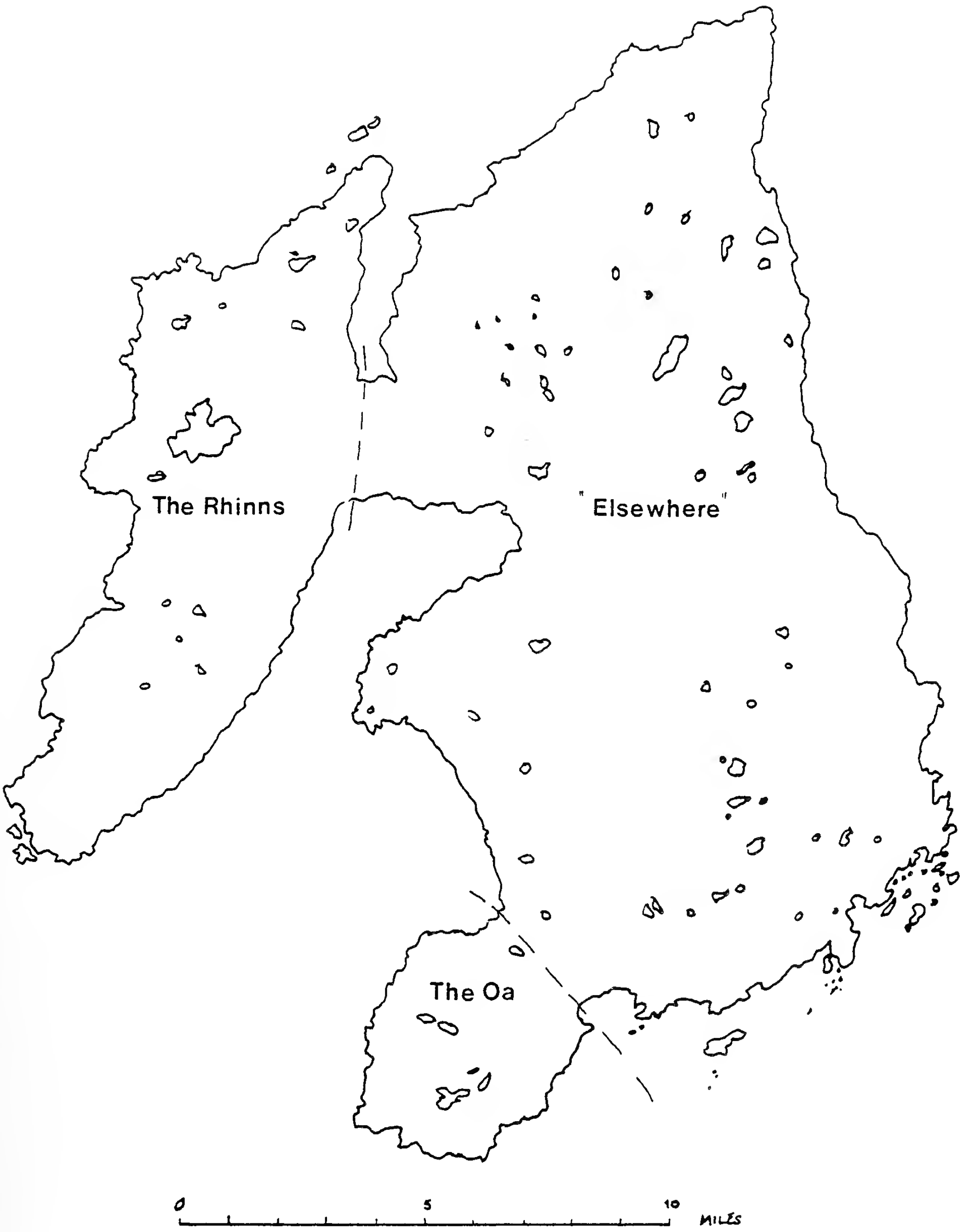

Figure 2

Map of Islay, showing the areas referred to in the text

Table 1

Nest site selection by Choughs on Islay
1981 and 1982

	1981			
	Oa	Rhinns	Elsewhere	Total
Sea cliffs	8	16	3	27
Inland cliffs	0	6	0	6
Buildings	0	5	4	9
Total	8	27	7	42

	1982			
	Oa	Rhinns	Elsewhere	Total
Sea cliffs	8	13	3	24
Inland cliffs	0	6	0	6
Buildings	0	5	7	12
Total	8	24	10	42

buildings. Elsewhere on the island, all nests were coastal and in buildings.

All nests examined were made exclusively of heather stems, with only one exception. This nest included some grass and straw in the heather structure, and was reported to have been the nest site of a Rock Dove *Columba livia* earlier in the year (D. MacFadyen, pers. comm.). Nests were usually situated adjacent to pasture grazed by either cattle or sheep, although on the Oa there was one coastal site backed by heather moor. This breeding pair flew inland to feed on suitable pasture about two kilometres away.

Changes in Distribution and Density of Breeding Choughs

From the 1976, 1981 and 1982 surveys, some changes in the density of breeding pairs in each of the fourteen 10-kilometre squares which cover the island can be followed (Figures 3 to 5). In all three years the main concentrations were on the south and west coasts of the Oa and the Rhinns. No inland areas or buildings were included in the 1976 survey, thus making direct comparison of some areas between years difficult, but general trends can be seen.

On the Oa, sixteen nests were found in 1976, fifteen in 1981 and seventeen in 1982. Although the area is difficult to search, and pairs could easily be missed because of the nature of the cliffs, the consistency of the results indicates that the distribution and density of breeding pairs has remained remarkably constant over this seven year period. There was no evidence of breeding pairs occupying buildings on the Oa in either 1981 or 1982.

On the Rhinns peninsula, twenty sites were located in 1976, 33 in 1981 and 26 in 1982. Five sites in the two latter years were in buildings, but no buildings were searched in 1976. Even if only coastal sites are compared over the years, however, the population has increased on the Rhinns (Figures 3 to 5). The increase has not been a steady one, thus suggesting that numbers fluctuate more here than on the Oa. The severe winter of 1981-82 may have had an adverse effect on recently established pairs, and storms destroyed at least two nests, only one of which was rebuilt in 1982.

Elsewhere on the island, four nests were found on the coast in 1976, but of the ten found in 1981 and eleven in 1982 only three were coastal. The remainder were all in buildings, at least three of which have only been occupied very recently. It appears, therefore, that there has been an increase in the number of breeding pairs in areas away from the Oa and the

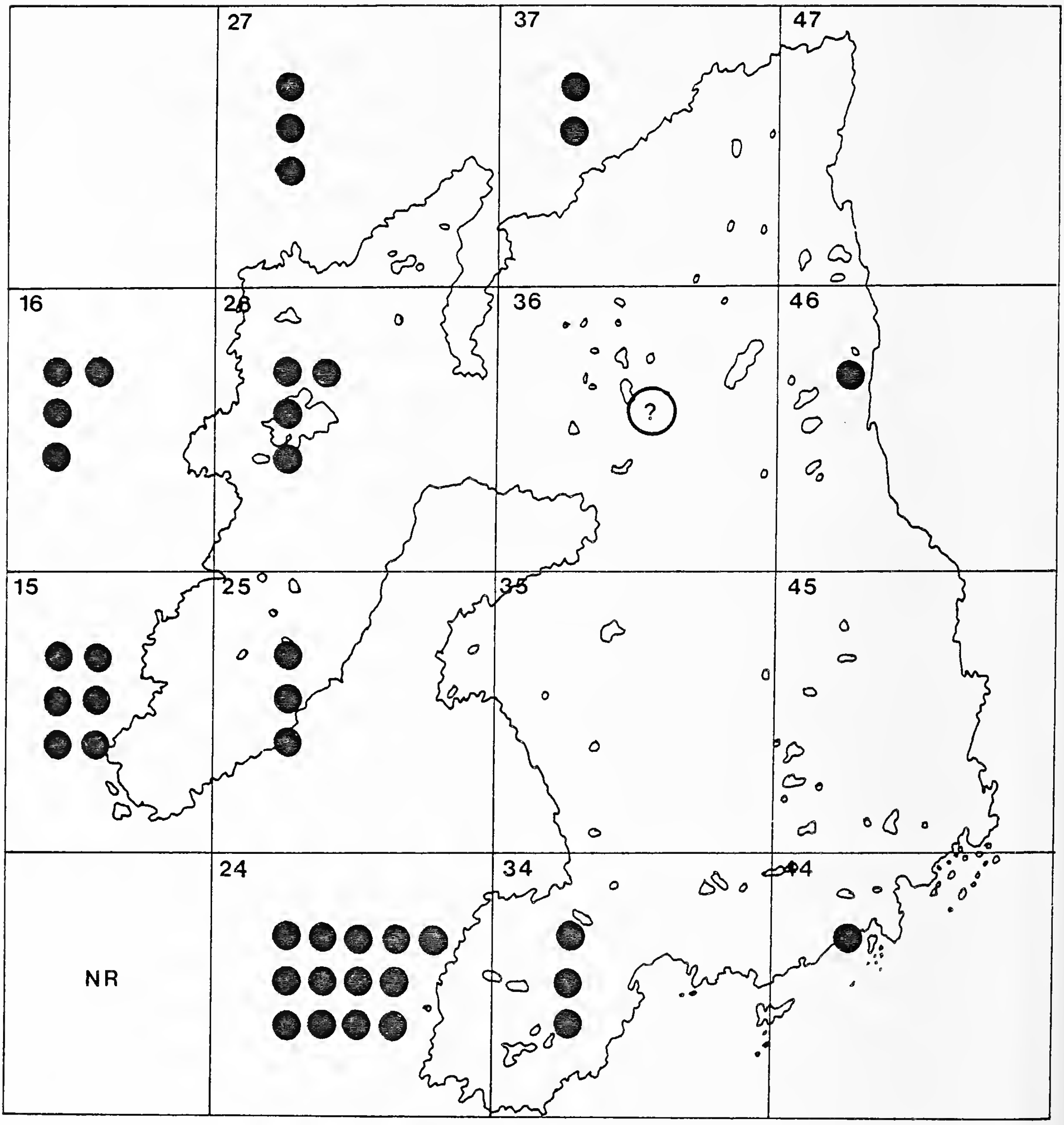

Figure 3

Number of breeding pairs of Choughs in each 10km square of Islay, estimated from the 1976 survey. N = 40.

(NR36 not surveyed in 1976)

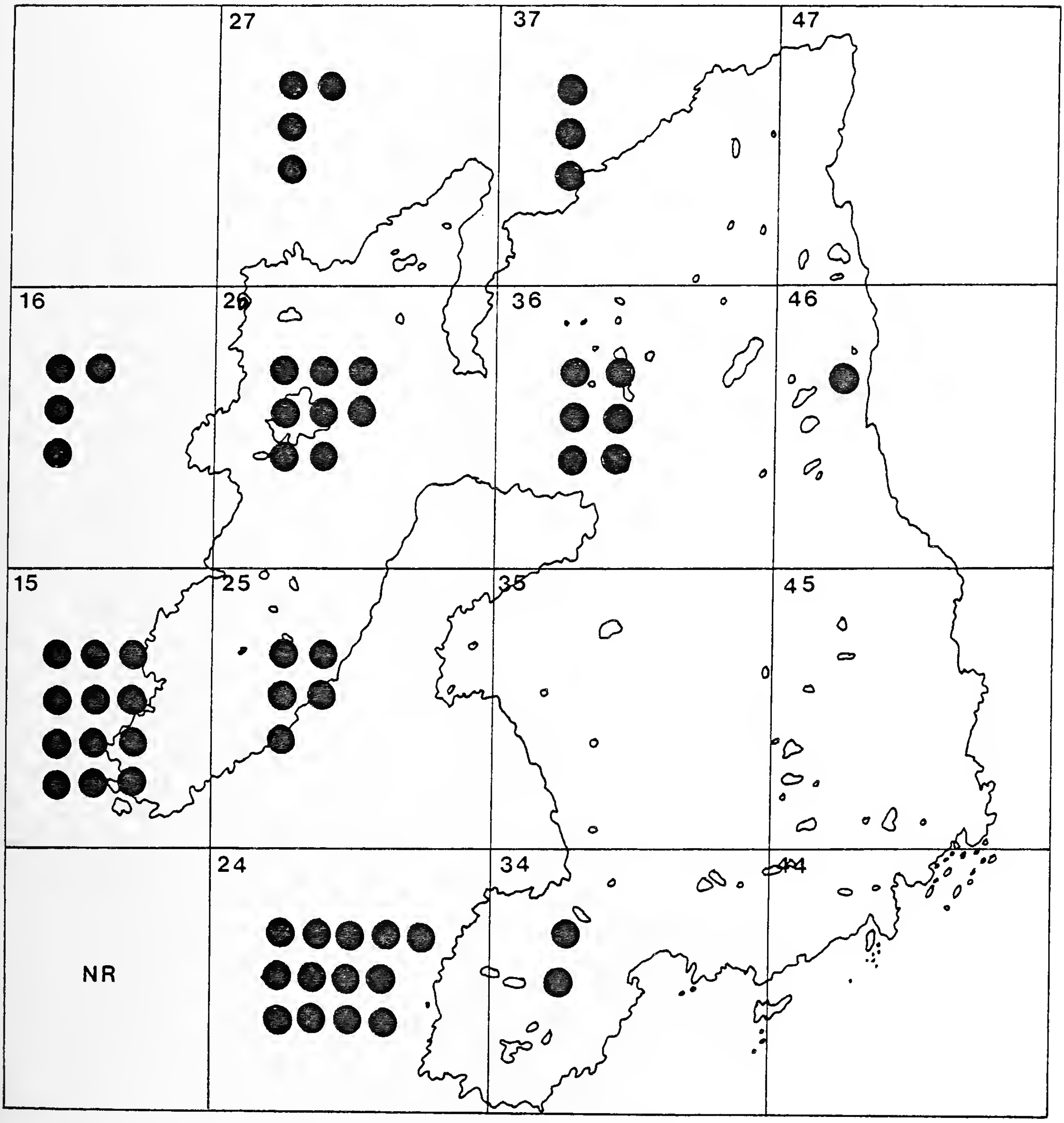

Figure 4

Number of breeding pairs of Choughs in each 10km square of Islay, estimated from the 1981 survey. N = 58.

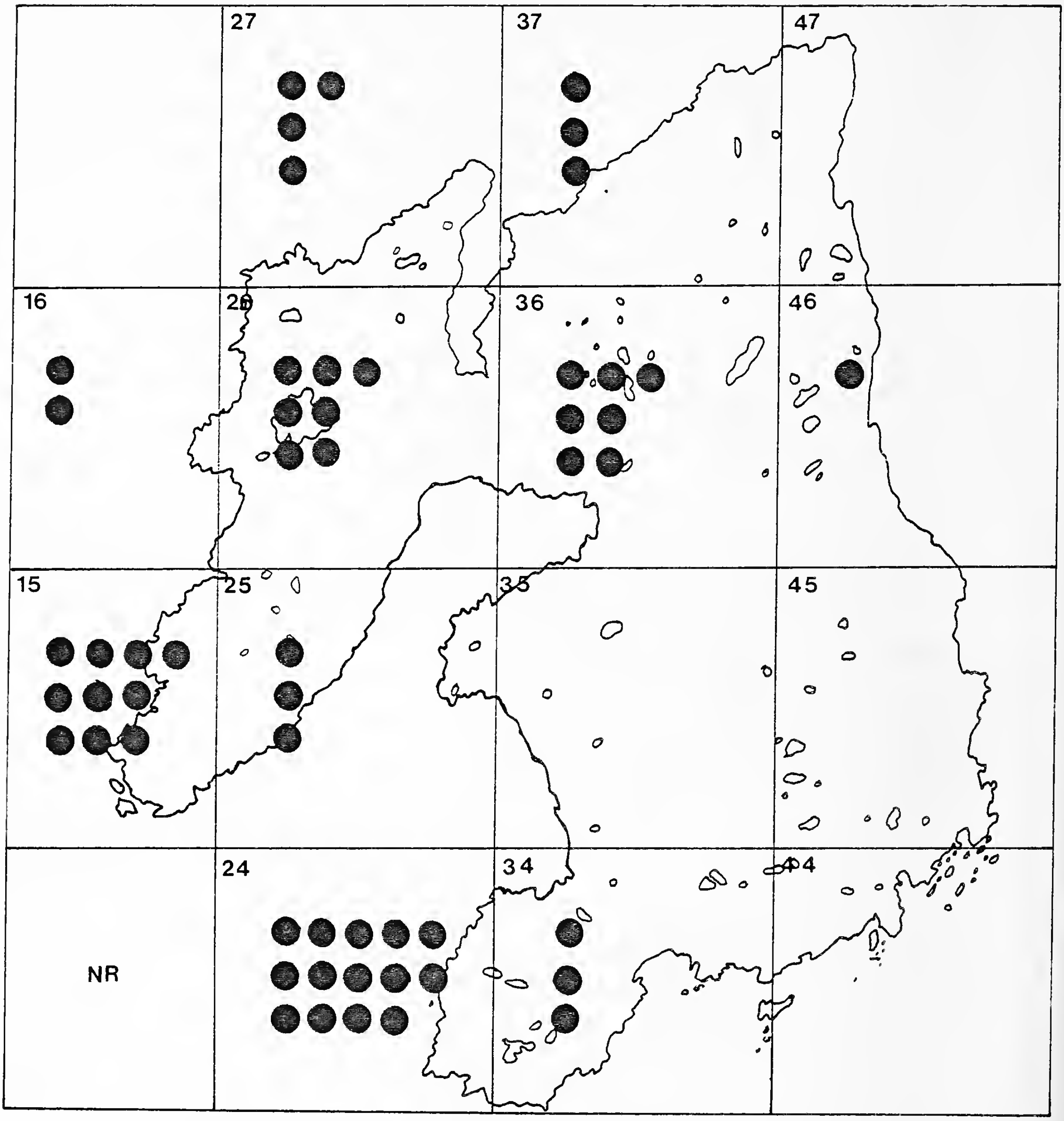

Figure 5

Number of breeding pairs of Choughs in each 10km square of Islay, estimated from the 1982 survey. N = 54.

Rhinns, which have always been the traditional areas.

Overall, since 1976 there has been an increase in the number of breeding pairs of Choughs on Islay, with this increase taking place mainly on the Rhinns and in north-east Islay. There appears to be a tendency for newly established pairs to occupy farm buildings. The first nest to be found in a building within recent years was in 1977 (C.G. Booth, pers. comm.), although the extent of this habit before then cannot be assessed. Intensive searching for barn-nesting Choughs was only started in 1980, when R.A.O. Hickling found five nests with nestlings present, and a further three with lined nests but no indication of breeding.

Breeding Success of Choughs on Islay

Information on clutch size, number of nestlings and of fledglings, together with details of mortality, was collected in 1981 and 1982. Additional records were taken from C.G. Booth's collected observations, R.A.O. Hickling's records, and B.T.O. nest record cards. The results are presented in Table 2.

Eggs were laid mainly between the second week of April and the end of the third week of May, with young in nests from the first week of May until the end of June. The number of eggs laid varied between three and six, with a mean clutch size of 4.38 ± 0.77 ($n = 24$), and up to five nestlings per brood were recorded (mean = 2.64 ± 1.27, $n = 53$). The maximum number of fledglings recorded was four, with an average of only 1.92 ± 1.34 ($n = 37$), thus indicating a high mortality rate in the nest. From the few nests followed from egg to fledging, only 26 young left the nest from a total of 77 eggs laid. This represents a mortality of 66.2%, resulting mainly from predation. At least ten of the 42 nests inspected in 1981-82 had been predated (23.8%), three of them in buildings. Nests in buildings would be vulnerable to attack from Brown Rats *Rattus norvegicus*, feral Cats *Felis silvestris* and Ferrets *Mustela putorius furo*, but those predated on the cliffs would be accessible only to agile, avian predators, such as the very numerous Hooded Crows *Corvus corone*. At one nest, egg collectors were suspected of taking the clutch of six eggs.

Nestling Choughs also suffer from disease and deformities. In 1980, a brood of three with deformed bills was ringed (R.A.O. Hickling, pers. comm.). The upper mandible was crossed over the lower in two of the nestlings, and the third had a short upper mandible. In another barn nest there was a single nestling which was wheezing and possibly suffering from gapeworm. During 1982, a single nestling was found with a swollen head and upper mandible, and in another nest the two

Table 2

Average clutch size, nestling numbers, and fledging success (± 1 SD) of Choughs on Islay

1981, 1982, and from all records

	Clutch size	Number of nestlings	Number of fledglings
1981	4.57 ± 0.53 (n = 7)	2.92 ± 1.60 (n = 13)	1.88 ± 1.41 (n = 16)
1982	4.25 ± 0.87 (n = 12)	2.35 ± 1.32 (n = 17)	1.85 ± 1.28 (n = 13)
All*	4.38 ± 0.77 (n = 24)	2.64 ± 1.27 (n = 53)	1.92 ± 1.34 (n = 37)

* Total of 1981 and 1982, plus all past records (see text).

young had sores on their tarsi caused by a sodden nest lining; water was running down the rock face and through the nest during a spell of very wet weather. Fresh wool was gathered to line the nest, but whether the young survived is not known.

Occasionally nests were found which were lined but in which no eggs were laid. A pair of Choughs remained in attendance throughout the breeding season in each case, and it is suggested that these nests were 'trials' built by young, inexperienced pairs. From three 'trial' nests in 1981, young were successfully reared in 1982, thus lending support to this idea.

At five nests in 1981 and at least four in 1982, a third bird was seen associating with the breeding pair. Although little is known about the role of this bird in the breeding season, at one site a third bird fed an incubating female in the nest territory and thus assisted the male in its task. Whether the third bird assists in the rearing of young has still to be investigated.

Feeding the Young Choughs

Observations on the feeding of nestling Choughs in a deserted farmhouse were made on three days between 22nd and 31st May 1981, when the young were about 18 to 27 days old. The times when one or both parents fed the young were recorded, and out of a total of 51 visits, 38% were made by both parents. The average time between feeds was 17.24 ± 12.04 minutes, and there was no significant difference in feeding intervals between days ($p > 0.05$). The timing of the intervals ranged from two to fifty minutes, and all observations were made between 11.00 and 17.00 hours B.S.T.

When the young Choughs leave the nests they are not very adept at probing into the turf and cow-pats for food, and are fed by the parents while they learn. By the end of four to five weeks, however, they can fed for themselves, and are then ignored by the adults when they beg for food.

Colour Marking Nestling Choughs

A ringing scheme was initiated in 1980, and is still continuing; thirteen nestlings were ringed in 1980, 35 in 1981, and 22 in 1982. In the latter two years, each bird was given a unique combination of colour rings, for subsequent individual identification. In 1981, three broods of colour ringed birds were seen feeding with their parents in the vicinity of the nest sites in June and July, and one brood was similarly seen feeding with the parents in 1982. Another individual, ringed as a nestling in 1981, was subsequently seen in March 1982 in a flock of seven, only one kilometre from the nest site where it had been ringed. Later, in October 1982, it was feeding in a flock of six birds 10.6 km from the nest site, and by March 1983 it was paired to an unringed bird. This pair built a nest in a previously unused barn in north-west Islay, 11.5 km from the original marking site, and the ringed bird was later found incubating three eggs. Choughs can therefore breed at the end of their second year of life.

From recoveries of marked birds it appears that twelve nestlings failed to fledge, at least four because of predation; two were found within two kilometres of their nest site in the first winter of life; a further individual was recovered 17.5 km from its nest site in its first winter. No sightings of surviving Choughs in their first winter have been further than 3.5 km from the marking sites, but from recoveries it seems that they can travel considerable distances within the island. No recoveries have been made away from Islay.

Discussion

The results of this study of the breeding biology of the Chough on Islay indicate that although most nests are on the sea cliffs, some are found on inland cliffs and others in buildings. It is suggested that the habit of nesting in buildings has increased recently, since there are only occasional records of this habit prior to 1977. There are no known nests in buildings in Wales (Bullock *et al.* in press), although some nest in mines and quarries in Snowdonia. In Ireland the habit of nesting in buildings is widespread (Bullock *et al.* 1983b), and on the Isle of Man nests have been found on a boathouse window ledge, and in the firegrate and wall of ruined lighthouses (Rolfe 1966). With the greater number of derelict houses on Islay in recent years, buildings appear to be increasingly used as nest sites.

The breeding density of Choughs was highest on the south-west coasts of the Oa and the Rhinns. Few pairs nested on the north-east or east coasts, where the cliffs are backed mainly by heathland (dominated by *Molinia caerulea* and *Calluna vulgaris*) which does not provide suitable feeding (Bullock 1980, Warnes 1982). In addition, on the east coast there are few suitable nesting caves or crevices on the cliffs.

The effect of the severe winter of 1981-82 on the Chough population of Islay is difficult to assess. In mid-Wales there was evidence of increased mortality during this winter, thus resulting in a fall in the number of breeding pairs (Bullock *et al.* in press) in 1982, and this may also have occurred on the

Rhinns although the reasons remain undetected.

The mean clutch size of Choughs on Islay is significantly higher than that on the Isle of Man and in Ireland (Bullock *et al.* 1983a), but not significantly different from that in Wales (Isle of Man = 3.39 ± 1.13, n = 49; Ireland = 3.76 ± 0.95, n = 87; coastal Wales = 4.27 ± 0.76, n = 33; inland Wales = 4.09 ± 0.90, n = 43). Despite this large average clutch size on Islay, the fledging success of Choughs was significantly lower than in Wales or Ireland, although similar to the number of fledglings on the Isle of Man, where the average clutch size is low (inland Wales = 2.05, coastal Wales = 2.68, Ireland = 2.85, Isle of Man = 1.88).

Although the reasons for the high mortality rate of nestlings and low fledging success are largely unknown, a contributory factor may be associated with the siting of nests in barns. Several nestlings either fell to their death, or were unable to return to nests if they climbed out, whilst others were predated. If, however, as suggested by the observations on a marked bird, many barn-nesters are young inexperienced pairs using non-traditional sites, these Choughs may lose young through their inexperience. Additionally, the increase in the Ferret, feral Cat and Hooded Crow populations may account for the high predation rate.

The irregularity in the feeding times of nestlings on Islay was also noted on the Calf of Man and Spanish Head (Williamson 1959), where the intervals ranged from three to sixty minutes (mean = 21.17 ± 19.93 minutes, n = 18). On Bardsey Island, however, feeding was at regular intervals at one nest (Cowdy 1962). This variation in feeding interval was said to result from differences in the distance to feeding grounds (Holyoak 1972), although variation in distribution and quality of food items may also affect the collection rate and thus influence feeding intervals. There are also differences in feeding behaviour of Chough parents, since on the Calf of Man (Whittaker 1947) and on Bardsey Island (Cowdy 1962) both parents always arrived together to feed the nestlings, whereas on Islay only 38% of visits were by the pair. The samples are too small to suggest regional variations.

Once fledged, the young Choughs on Islay were fed for at least a week, but were feeding independently by four to five weeks. This agrees with observations by Holyoak (1972), but on Bardsey the young were fed for only one week after fledging (Cowdy 1960). Again, samples are too small to indicate regional differences.

In conclusion, Islay has the largest population of Choughs in Scotland and, despite a poor fledging success, appears to be sustaining itself, and also probably increasing in some areas of the island. Future expansion will depend to a large extent on the maintenance of permanent pastures for feeding (Warnes 1982), and the availability of suitable nest sites, principally in buildings.

Acknowledgements

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SHORT NOTE

ANOTHER LEATHERY TURTLE IN THE CLYDE AREA

On 1st September 1981 a Leathery Turtle *Dermochelys coriacea* was seen in the Clyde between Toward Point and Gourock by Dr. A.J. Baillie and a colleague. This was duly reported in some detail in the *Western Naturalist* (10: 24).

On 9th July 1983 another Leathery Turtle was seen near the entrance to Loch Fyne by Mr. Andrew Pettigrew and his family, who were yachting on the Clyde. The turtle was seen in very calm conditions, and Mr. Pettigrew has supplied an excellent description which leaves no doubt as to the correctness of the identification. On 14th July 1983 Dr. A.J. Baillie, who reported the 1981 Leathery Turtle, and Mr. B. McGuigan were canoeing in the Kyles of Bute and also saw a Leathery Turtle, in the west Kyle some two miles south of Kames. They managed to approach to within a few feet, and again an excellent description was taken which leaves no doubt as to the identification.

There seems little doubt that these two accurate records, plus other reported sightings, less well authenticated, refer to the same animal.

The only previous Clyde records of the Leathery Turtle were in 1875, 1959 and 1961 (*Western Nat.*, 5: 57-58), but it is also worth noting that one was found dead on Jura in September 1978 (*Western Nat.*, 7: 101). It has been suggested that slight changes in climatic conditions may account for the increased number of records of what was formerly considered to be a very rare creature.

J.A. Gibson

BOOK REVIEWS

GIBSON, J.A. and RAINIER, IDA. (1983). *Atlas of Mid-Argyll Vertebrates.* Lochgilphead: Natural History and Antiquarian Society of Mid-Argyll.

GIBSON, J.A. (1983). *Atlas of Renfrewshire Vertebrates.* 2nd Edition. Paisley: Renfrewshire Natural History Society.

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GIBSON, J.A. (1985). *Atlas of Lanarkshire Vertebrates.* Glasgow: Clyde Area Branch, Scottish Wildlife Trust.

It is really unnecessary to write a lengthy review of these four additional volumes in such a well-known and highly regarded series of natural history publications, but it is a genuine pleasure to do so. Dr. Gibson is the pioneer of all biological recording in this country, and is noted not just for the immensity of his own contributions, but also for everything he has encouraged others to do. His remarkable series of Vertebrate Atlases and Regional Check-Lists has simply revolutionised all our previous ideas and standards of natural history recording, for nothing like them has ever appeared before. The depth of knowledge, field and bibliographical experience, intensive research, and sheer hard work necessary for the creation of such a series is quite unparalleled in the entire history of the subject, and we may all well wonder how on earth we managed previously.

The format of these Vertebrate Atlases is now well known, and these four new volumes in the series follow the same pattern and maintain the same high standard. After a general Introduction, two sets of 10km-square distribution maps are given for every species of mammal, breeding bird, reptile, amphibian, and freshwater fish which has ever been recorded for each area. The first of the maps gives the historical picture, in quarter, half, three-quarter and full centuries from 1800 to date, and the second map sets out what is believed to be the known distribution at the present day. Each 10km square is numbered, and different type is used for each date category, so that past and present distribution can be seen at a glance. All this work, of course, was pioneered by Dr. Gibson for the Clyde faunal area, and is still virtually unique in our country, although others, with Dr. Gibson's encouragement, are now beginning to follow his lead and example.

At all times, however, it is emphasized that Atlas distribution maps are no real substitute for properly researched and written accounts along traditional lines; instead they properly supplement each other. So a precisely detailed bibliography is given for each area covered. This alone is an invaluable contribution, and, not surprisingly, it also reveals that, during the past fifty years, virtually all the major accounts of Clyde vertebrates, for both the entire Clyde area and all the minor faunal areas, have been written by Dr. Gibson himself. This is not, of course, the purpose of the bibliographies, but it does demonstrate the incalculable personal contribution made to our existing knowledge.

The first of these new Atlases, by Dr. Gibson and his colleague Mrs Ida Rainier, the well-known Argyll naturalist from Achnamara, covers Mid-Argyll, a title which has presumably been chosen to reflect the name of the Natural History and Antiquarian Society of Mid-Argyll, who have published this Atlas. One of the most praiseworthy features of this remarkable series of Atlases is the way in which the Clyde Area Branch of the Scottish Wildlife Trust and the local natural history societies throughout Clyde have worked together so closely on Clyde vertebrate recording during the past fifteen years. It is no coincidence that Dr. Gibson has been Chairman of the Clyde Area Branch of the S.W.T. for the past fifteen years and is also a member, indeed now usually an Honorary or Life member, of all Clyde natural history societies; he has acted as the driving-force and catalyst which has created such close cooperation, and the wonderful end results are here for all to see. It is to be hoped that this invaluable cooperation continues after Dr. Gibson retires as S.W.T. Chairman, which he has announced he will be doing next year.

The two districts of Clyde Argyll covered by this Mid-Argyll Atlas are Knapdale and what is called Upper Loch Fyne, i.e. the area of Argyll lying between Loch Fyne and Loch Awe, and unquestionably consist of the areas of Clyde which are most difficult to work and from where most additional information was required. Much of the area is devoid of any vehicular access, and from the natural history point of view was hitherto virtually uncharted. The authors have drawn upon their own deep personal experience of the area, plus what they have been able to glean from an extremely wide circle of local contacts, and at the end of the day they have covered the area incredibly well. Much of the information given here is actually appearing in print for the very first time. The usual precise bibliography is also given, but since much of the previously published work was included within written accounts of the entire Clyde area, and not treated separately for Mid-Argyll, the authors have also provided much additional information by way of supplementary notes, which in the circumstances are particularly valuable. Speaking personally, as one who has spent many years hill-walking in the area, the amount of distribution data packed into this Atlas is nearly beyond belief, and has completely transformed our previous knowledge of its natural history.

The other three Atlases cover the entire lowland area of Clyde, although it is really fortuitous that they are all being reviewed together. It does, however, permit a very valid comparison to be made between known distribution in highland and lowland Clyde. One of the most interesting aspects of Clyde distribution, which also makes it such a difficult area to cover properly, is the division of the entire Clyde faunal area by the river Clyde into highland and lowland areas, with the islands somewhat in between and showing features of each. The Clyde Atlases now demonstrate this in a very clear-cut way.

Renfrewshire, of course, has been covered before, in 1970. This was the very first complete Vertebrate Atlas of an entire county ever to be published in our country, but, as befitted its pioneer status, at that time only one distribution map was given for each species. Here we now have it reissued by the Renfrewshire Natural History Society, but completely revised and brought up to date, with two maps for each species, uniform with all the other Clyde Atlases. Unfortunately, during the transfer of the records from one to two maps, a few transcription errors crept in which were not noticed until after the main section of the Atlas had been printed, so an errata slip had to be included. These should all have been carefully inserted, but since this is the first time this has occurred for any Atlas, we have been asked to draw attention to this so that readers can ensure that the necessary corrections have been made.

The Ayrshire Atlas is published by the Ayrshire Biological Records Centre, based at the Dick Institute in Kilmarnock, and is dedicated to the Kilmarnock Glenfield Ramblers Society in recognition of the 100th anniversary of the Society. Some of us had the good fortune to attend the Society's centenary meeting at which the publication of the Ayrshire Atlas was also announced, and it makes a fitting tribute to an old-established and hard-working society. The Lanarkshire Atlas, published by the Clyde Area Branch, S.W.T., has just arrived, in proof copy form, and completes the trilogy for lowland Clyde. All three, with their comprehensive maps and bibliographies, now provide a picture of lowland Clyde vertebrate distribution with a wealth of detail hitherto completely unknown.

When one compares highland and lowland Clyde distribution, there are some features which are immediately obvious, since they have always been well known: for example, Red Deer, Wild Cat, Pine Marten, Golden Eagle, Adder, and Charr, are virtually confined to the highland part. Surprises are in store, however, with the comparative distribution of some other species, e.g. the Common and Palmate Newts. Our old friend the Hedgehog also used to be virtually confined to lowland Clyde, and the fact that it is now so widespread in the highland part, according to the authors, follows the frequency with which it was transported as a pet towards the end of last century. The pages of the Atlases are full of such interesting contrasts, and it is a great time waster to sit down and make comparisons.

I well remember my own first experience of these Clyde Atlases, that for the Island of Arran in 1975. I had known Arran since my early childhood, and my wife and I had been going on holiday to Arran several times a year for over forty years, so that I fondly imagined there was little we did not know about the distribution of Arran wildlife, but the arrival of the Arran Atlas ten years ago was a revelation, like a vast window being opened, which instantly changed our appreciation of the entire island. I have no doubt that these Atlases will have given many other naturalists the same experience for areas of Clyde which they previously thought they knew well.

No price is given on these Atlases, but they can be obtained for £5.00 each by the general public, an extremely modest price nowadays and the bargain of the century when one considers the wealth of information they contain. Members of the S.W.T. or any of the local natural history societies can obtain them at much reduced prices, on application to the various Secretaries or from the Scottish Natural History Library.

For two generations Dr. Gibson has been at the centre of all Clyde natural history, and has long been known for the detailed accuracy of his pioneer vertebrate recording; it is therefore wonderful to have the end results of all his precise work now available in such easy reference form. One can only be happy to repeat and paraphrase what has already been said by reviewers of previous volumes in the series, that "these Atlases set an entirely new standard for natural history recording, at which other local recorders will now have to aim, ...and are clearly the most detailed works on vertebrate recording ever published in Scotland. Nothing like this continuing series has ever appeared before, for the Clyde or any other Scottish faunal area. Each volume represents genuine pioneer work of the highest order, and the entire series cannot be recommended too strongly". The last in the series of regional Atlases, that for the Loch Lomond Area, is scheduled for next year, to be followed in due course by the complete *Atlas of Clyde Vertebrates*. By that time we will certainly have "a survey and a working tool which a few years ago was quite unimagined".

R.G. Ellis

HUNTER, CLARK. (1983). *The Life and Letters of Alexander Wilson*. American Philosophical Society, *Memoirs* Series, Volume 154. Philadelphia. Pp. xii + 460. 10" x 6.75". Price $40.00.

Just occasionally one receives for review a book which it is virtually impossible to fault, and let me say straightaway that Clark Hunter's Life and Letters of Alexander Wilson comes into this rare category. Clark Hunter, a retired businessman from the town of Paisley, Wilson's birthplace, has made a lifetime's study of Alexander Wilson and his work, and has long been rightly regarded as the ultimate authority on the subject. This volume is the outcome of the author's great depth of existing knowledge, a sharply analytical although sympathetic approach to his subject, and over ten years of new intensive research.

After a brief but useful introduction, which pays generous tribute both to previous historians and to all who have assisted the author in his present work, the book is divided into two main parts. Firstly there is a 113-page account of Alexander Wilson's life. This is a meticulously researched, excellently written, comprehensive account, which comprises the author's main original contribution. Clark Hunter has an enviable literary style, and his account of Wilson's life holds one's interest throughout and could well stand by itself as an important literary and historical achievement. It would be idle to pretend that Wilson would be much remembered today had he not played such a pioneer role in the development of American ornithology, but he was also an interesting and complex man who deserves our attention, and the reasons which caused him to leave Scotland in a hurry have been carefully unravelled and set out by the author, with a series of useful appendices describing the various legal cases; also included are copies of

Wilson's naturalisation certificate and his last will and testament. Never before has Wilson's life, both in Scotland and America, been described so scrupulously, and clearly Scotland's loss was America's gain.

Part two consists of a 290-page edited account of Wilson's letters, many of which are now printed, or printed complete, for the very first time, along with many important explanatory notes, plus a glossary of Scottish words which Mr. Hunter has thoughtfully provided for 'foreign' readers. In America, Wilson set out "to make a collection of all our finest birds", and in pursuit of this goal he travelled through much of the eastern part of the United States, often undertaking prodigious journeys on foot. On one such journey he covered 1,200 miles on foot, averaging some thirty miles a day, yet still managed to collect and draw his birds. His letters make fascinating reading, and well document the joy he felt at each new discovery, as well as the terrible physical hardships he endured.

Here it is also important to emphasize just how much detailed detective work Clark Hunter had to carry out to discover the whereabouts of many of the Wilson manuscripts. Because the repositories of Wilson's letters had never previously been recorded, Mr. Hunter had tremendous difficulty in tracking them down, a task, however, which he tackled with true Scottish determination. The *National Union Catalog of Manuscript Collections* was of little or no help, for it contained no record of Wilson manuscripts, for example, at such major sources as the Library of Congress, Harvard University, Pennsylvania Historical Society, or the American Philosophical Society. After many years of tenacious work, however, Clark Hunter found and catalogued them, and eventually almost all proved to be in institutions in Scotland and America. The lengthy list of acknowledgements given by the author, therefore, is not just generous, but is also a tribute to his own tireless industry for well over a decade.

The end result is the most critically detailed, yet understanding, account of Alexander Wilson's life and place in ornithological history which has ever appeared. Over the years Clark Hunter has written many articles on Wilson, but with this comprehensive volume he has performed a signal service for all other historians of natural science. Anything which might be added in the future (for no doubt the odd little item may be discovered which has slipped through even the Hunter net), or any later assessment of Alexander Wilson's achievements, will now be firmly based on Clark Hunter's pre-eminent scholarship.

Possibly for the first time, Clark Hunter's book makes it clear that William Bartram, the pioneer American naturalist from Philadelphia, was Alexander Wilson's mentor as artist/naturalist and writer, but a central theme throughout the book is also just how much Audubon owed to Wilson, which any unbiased reader of the available evidence would now conclude must have been a very great deal; in fact few would disagree with Hunter's view that without Wilson's pioneer work there might have been no Audubon's *Birds of America*, or else it would ultimately have appeared in a very different or reduced form. Certainly there is no evidence that Audubon ever considered an ornithological work before he met Wilson at Louisville in 1810 and saw the first volume of Wilson's *American Ornithology*.

Wilson well deserves his title of 'The Father of American Ornithology', and his abilities were certainly much more broadly based than Audubon's. Wilson's prose in the bird essays of his *American Ornithology* is fine literature and, possibly uniquely in the ornithology of his time, he also wrote all these essays himself. Audubon, however, employed the distinguished Scottish naturalist, William MacGillivray (later Professor of Natural History at Aberdeen University), to "revise and correct" the *Ornithological Biography* at two guineas per sheet. In the illustrations, Wilson aimed for accuracy and Audubon for dramatic effect, but for the magnificent plates of the *Birds of America* Audubon had massive assistance from many other artists who drew very many of the fine botanical landscapes and backgrounds, and sometimes even the birds. Audubon was a severe taskmaster of engraver Havell's colourists, but, as far as we know, did none of the colouring himself. Wilson, on the other hand, had no such outside aids and often had to colour the printed plates himself; in fact, towards the end of his life he was the sole colourist.

The entire book has been most tastefully produced by the American Philosophical Society, and forms Volume 154 of the Society's *Memoirs* series. The elegant type face used is Monotype Bell, an 'accurate adaptation of a late eighteenth-century British type design for the printer and publisher John Bell', and the first-class acid free paper is 'Rising Book Laid'. The many excellent illustrations in black and white and colour, maps, and wood engravings are all splendidly produced. The layout is spacious, there is an excellent dust-jacket, and the complete volume is a most sumptuous publication which is, quite simply, a joy to handle. In other words, for once we have a book where the excellence of the production matches the excellence of the contents, and nowadays one does not find this too often.

In summary, this is a simply magnificent work of scholarship and intellectual research. In the past, there have undoubtedly been other natural historians who have carried out their appointed tasks with comparable care, patience, perseverance, diligence and critical assessment. In this instance, however, what possibly raises Clark Hunter's work above the high level of some exceedingly distinguished colleagues is his personal involvement and sympathetic feeling for Alexander Wilson as a man, and perhaps this in turn stems from his own Scottish upbringing in a not too dissimilar tradition. It is virtually impossible to praise this book too highly, and anyone even remotely interested in the early history of ornithology, both here and in North America, should try very hard to obtain a copy.

J.A. Gibson

[This book, of course, is published in Philadelphia, but copies can be obtained from Messrs Wheldon and Wesley, Natural History Booksellers, Lytton Lodge, Codicote, By Hitchin, Herts SG4 8TE, who act as British agents. The current price is £28.50 post free. - Editors.]

THE SCOTTISH NATURALIST
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A Journal of Scottish Natural History

With which is incorporated *The Annals of Scottish Natural History*
and *The Western Naturalist*

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